REVISION OF THE GENUS EUGNORISMA BOURSIN, 1946, PART II. TAXONOMIC NEWS, BIOGEOGRAPHIC AND PHYLOGENETIC CONSIDERATIONS WITH DESCRIPTIONS OF TWO NEW GENERA (LEPIDOPTERA: NOCTUIDAE)

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Besides the descriptions of some new Eugnorisma taxa (Eugnorisma goniophora sp. n., E. caerulea rubicunda ssp. n., E. gaurax funebris ssp. n. and E. asad plantei ssp. n.), the second part of the revision contains some changes in the taxonomic relegations of some 'Paradiarsia', 'Hermonassa' and 'Eugraphe' species. The phylogenetic and zoogeographical analysis of the genus and some related genera, with the descriptions of two new genera, Ledereragrotis gen. n. and Pseudohermonassa gen. n. are given. With original '10toplates and 78 figures.

Introduction

During the taxonomic and phylogenetic analysis of Eugnorisma and its relatives we have described some new taxa. It was also demonstrated, that numerous genera, classified formerly — with few exceptions — as belonging to the tribe Agrotini (Kozhanchikov, 1937) have usually a specialized, long, tubular vesica penis which can be accepted as true synapomorphy of these genera e.g. Euxoa Hübner, Agrotis Ochsenheimer, Trichosilia Hampson, Dichagyris Lederer, Yigoga Nye, Hemiexarnis Boursin, Parexarnis Boursin, Protexarnis McDunnough, Chersotis Boisduval, Rhyacia Hübner, Standfussiana Boursin, etc. Their other features of taxonomic importance are as follows: the more sclerotized frons, often with conspicuous protuberances, the relatively short tibiae of the forelegs (in most cases shorter than the first segment of the tarsus), the relatively broad, quadrangular or rounded shape of the valvae, in most cases with cucullus and corona (but the reduction of these may often be a convergent feature).

The larvae belonging to these genera are mostly of "cutworm" type, terricolous and connected — with relatively few exceptions — to montane or eremic grassland habitats. Here is the place to point out that some plesio-

morphic features (e.g. the presence of the cucullus and the corona, the ampulla as in *Diarsia* or in some *Dichagyris*) cannot have the taxonomic value which was attributed to them in some earlier publications of the systematics of Noctuinae. A parallel case of a not closely related group (the genus *Auchmis* HÜBNER) was analysed in an other paper. (RONKAY & VARGA 1990).

It has been shown that Eugnorisma Boursin suggested being related to Protexarnis McDunnough in the original description, cannot belong to the tribe Agrotini but is closely connected to Eugraphe Hübner, Paradiarsia McDunnough and Xestia s. l., etc. At the same time it became evident that the great number of species, referred formerly to Hermonassa Walker, 1865 (Boursin 1967) in fact belongs to three different major groups. Two of them are described here as new genera.

I. TAXONOMIC PART

1. Descriptions of some new taxa

Eugnorisma goniophora VARGA, RONKAY et HACKER sp. n. (Plate I: 1--2)

Holotype: male, "Pekistan. Baltistan, Gilgit 1600 m, $35^{\circ}53' \text{ N}$, $74^{\circ}21' \text{ E}$, 5. X. 1988, leg. Hacker", slide No. 5479 Varga. Deposited in coll. Hacker (Staffelstein). — Paratype: 1 female, from same locality and data; coll. Hacker. Slide No. 3331 Ronkay.

Description — Wingspan 35 mm, length of forewing 17 mm. Head and thorax dark grey mixed with some blackish-brown hairs, palpi laterally dark brown. Ground colour of forewings dark grey, strongly suffused with dark brown. Transverse lines obsolescent, double, less sinuous. Subbasal line only a blackish spot at costa antemedial line oblique, dark grey, defined by a fine black line on outer side. Postmedial line slightly sinuous, dark grey, filled with a bit lighter grey, subterminal line a diffuse, waved, brownish shadow with a dark brownish patch at costa. Orbicular and reniform stigmata large, finely encircled with whitish-grey and filled with grey. Orbicular oblique and flattened, reniform more or less moon-shaped; claviform absent. Dark triangles of cell strong and sharp, black with slight bronze shade. Terminal line ochreous-whitish, cilia dark grey. Hindwing nearly unicolorous fumous grey, veins suffused with brown, cellular lunule and transverse line absent. Terminal line whitish, cilia dark grey. Underside of fortewing patternless dark grey, hindwing whitish with intensive greyish suffusion, cellular lunule a very pale spot, transverse line an interrupted, grey shadow. Female similar with a bit darker colouration.

Male genitalia (Figs 1-2): uncus relatively short, curved, tegumen less high, fultura inferior subtriangular, vinculum V-shaped. Valvae narrow,

elongate, apex rounded with a small, less pointed lobe on ventral edge. Pollex small, pointed, sacculus short and wide, clavus absent. Harpe wide-based, short and thick, strongly curved. Aedeagus short, cylindrical, proximally weakly curved, carina less developed, without teeth. Vesica tubular, curved, without spinules, basal diverticulum large and wide, cornutus huge, wide-based, thorn-like.

Female genitalia (Figs 6—7): ovipositor short and wide, gonapophyses short. Ostium bursae wide, strongly sclerotized, ductus bursae strong, flattened and not folded, with two slight rugae on ventral surface, anterior part granulose. Bursa copulatrix very large and spacious, elliptical, apex finely rugulose.

The new species is similar in its appearance to a very dark specimen of a species of the *chaldaica*-group (except *tamerlana*) but it has dark hindwings. It differs from the related *E. eucratides* by darker ground colour of both wings, the lack of the reddish shade and the different shape of the blackish triangles of the cell.

The configuration of the male genitalia is very different from that of the chaldaica-group and shows close relationship with E. eucratides and xestioides by the general shape of the valva, the absence of macrotricha on the pollex and the presence of a large, wide-based cornutus on the basal diverticulum. The specific differences can be found in the structure of the carina—simple in goniophora, with a dentated lamina in xestioides and with a strong tooth in eucratides—, the spinulose field of the vesica—present in xestioides, absent in goniophora and eucratides—, the shape and size of the cornutus, the valvae and the harpae (see Figs 3—5).

The configuration of the female genitalia differs from the other Eugnorisma species (with the exception of E. coryphaea Püngeler) and E. eucratides Brsn. by the nonfolded, flattened, but strongly sclerotized ductus bursae, as a plesiomorphic feature in the genus.

Eugnorisma caerulea rubicunda VARGA et RONKAY ssp. n. (Plate I: 4)

Holotype: male, Margelan, slide No. 5510 Varga; coll. Zoologische Staatssammlung Munich (= ZSM). — Paratypes: 1 male, Altai (coll. ZSM), 1 male from the same locality (coll. ZMHU), 1 male, Lepsa, 2 males, Saisan (coll. ZMHU), 1 male, Lepsa, 2 males, Saisan (coll. ZMHU); 1 male, Sibiria, ex coll. Neuburger (coll. HNHM).

Description — Wingspan 36—37 mm, length of forewing 15—16 mm. The new subspecies differs from the nominate race externally rather strongly by the following features: the specimens are relatively small and narrow-winged. The light bluish-grey ground colour is evenly suffused by

a rosy-reddish shine. The transverse lines are less marked, fine. These characteristics give the specimens a special, *chaldaica*-like appearance, therefore, a part of them were misidentified in the collections. The configuration of the male genitalia is very similar to that of the nominate *caerulea* Wagner, but the valvae are relatively narrow, angulate, the pollex is more acute, the harpae are somewhat more slender and the spinulose field of the vesica is more conspicuously saccate (Figs 8–21).

This subspecies displays a diametral contrasting tendency with the taxa E. caerulea kurdistana and E. caerulea isabellina, because the latter two can be characterized by the missing of the reddish colouration, the more sharp and distinct transverse markings and the broader shape of the wings. We think that E. caerulea has been historically separated into two main chains of geographical races and the genetic isolation between the extreme forms of these race-groups may be nearly on the specific level. E. c. caerulea and E. c. kurdistana have an overlapping distribution pattern in some parts of E Turkey (e.g. in the Provinces Bitlis and Bingöl) and only very few transitional (?) specimens are known. Therefore we re-examined the $\partial \partial$ and $\partial \varphi$ genitalia of all caerulea-subspecies but were not able to find any decisive differences.

Nomenclatorical notes — In Kocak's (1983) the name "Agrotis Chaldaica var. Caerulea Wagner, 1932" cannot be used as a valid name as it is preoccupied by Agrotis coerulea Guenée, 1868, and he gave Eugnorisma buraki nom. n. as replacement name for the former taxon. We cannot agree with this statement because the species names are not exactly the same (caerulea versus coerulea) and because both taxa were described with subgeneric classification which are different in the two cases. Wagner placed his taxon into the subgenus Rhyacia ("Agrotis [Rhyacia] chaldaica var. caerulea") since the Guenée's coerulea was originally arranged into the subgenus Spaelotis, consequently the original combinations are not the same in the two cases under discussion. Therefore, we can use Eugnorisma caerulea (Wagner, 1932) as the correct name for this well-known species and no replacement name is necessary.

Eugnorisma asad plantei VARGA, RONKAY et HACKER ssp. n. (Plate I: 5)

Holotype: male, "Pakistan, Baltistan, Babusar Pass, Nordseite 1650 m, 6. X. 1988, leg. Hacker", coll. Hacker. — Paratypes: numerous males and females from the same locality, further specimens from Pakistan (Karimabad, Nilt, Passu, Gilgit, the Kaghan valley), Kashmir, India (Ladakh: Kharbu, Drass, Lotsun), coll. Hacker, Peks, Plante, Varga, Vartian, Weigert, HNHM and ZSM. Slides Nos 3765, 5534 Varga (males).

Description — Wingspan 36—42 mm, length of forewing 17—20 mm. The new subspecies differs from the nominate asad by its larger size, broader shape of wings, much darker, fuscous-grey ground colour with the absence of the light rosy-brown shade being characteristic for asad asad. Orbicular spot is usually conspicuously encircled with whitish-grey. In the configuration of the male genitalia asad plantei has distally less arcuate valvae and the costal lobe is reduced or absent (see the Figs 85—87 in the first part of the revision).

The new subspecies has a larger area as compared with the nominotypic one; it is distributed from NW Pakistan to Kashmir and Ladakh (? Nepal) and appears in large individual number in its habitats.

Eugnorisma gaurax funebris VARGA et RONKAY ssp. n.

Holotype: male, USSR, Uzhbekistan, Alai Mts, Dugobo, 30. IX. 1985, leg. et coll. Varga. — Paratypes: $1 \, 3$, $2 \, 2$ from the same locality and data, coll. HNHM and Varga. Slide No. 3337 Varga.

Description — Wingspan 29—31 mm, length of forewing 14—15 mm. The new subspecies is similar externally to the nominate subspecies, but is essentially darker, the ground colour of the head, thorax and forewings is dark grey with fuscous shade. The pinkish-rosy shade, typical for gaurax gaurax, is entirely absent; the colouration of the hindwings is also darker, suffused with brownish-grey.

This subspecies — without name and description — had been already mentioned in p. 220 of the first part of the revision and figured on Plate II., Fig. 32.

Distribution — The few known specimens of funebris were collected in a rocky, gorge-like valley on the northern side of the Alai Mts. at ca. 2500 m altitude; together with a series of E. puengeleri and some specimens of E. eminens and E. trigonica.

2. Taxonomic changes, new combinations

Eugnorisma eucratides (Boursin, 1957) comb. n. Eugnorisma xestioides (Hampson, 1905) comb. rest. Ammogrotis suavis Staudinger, 1895 comb. rest. Eugraphe miniago (Freyer, 1838) comb. n.

3. Descriptions of two new genera

The study of the generotype of *Hermonassa* Walker, 1865 (consignata Walker, 1865) and some close relatives has shown that the true *Hermonassa* Walker species have a very distinct genital configuration and they are not

related to Chersotis Boisduval, as suggested by Boursin (1967). It became evident (see Figs 26—32; 33—44) that two species, classified earlier as "Caradrina" (subg. Chersotis, cf. Kozhanchikov 1937, Zholotarenko 1971) or Hermonassa Walker (Boursin 1967 and manuscript) have tubular vesica also an other Agrotini features. For these two species: multifida Lederer, 1870 and difficilis Ershov, 1877, we erect a new genus described below.

Ledereragrotis VARGA gen. n.

Type species: Agrotis multifida LEDERER, 1870 -- Ann. Soc. Ent. Belg. 13: 46, t. 2, f. 10.

Diagnosis — Medium-sized, "Agrotis"-like moths, resembling externally to some *Chersotis* Boisduval species. Frons convex, moderately sclerotized, without protuberance. Abdomen depressed dorsoventrally. Male genitalia (Figs 26—32): harpe long and falcate, ampulla present, directed laterally; clavus reduced. Uncus relatively broad and long. Aedoeagus long and straight; vesica tubular and coiled. Female genitalia can be characterized by bilobate bursa copulatrix similarly to some related genera (*Dichagyris* Lederer, *Parexarnis* Boursin, *Protexarnis* McDunnough, etc.).

The new genus contains only two species, Ledereragrotis multifida LEDERER and L. difficilis Ershov, 1887, resp. These species are completely allopatric, the former one is distributed in the Central and Western Alpine semi-arid areas ("inneralpine Trockengebiete"), Asia Minor, Caucasus and Transcaucasia; the latter in the mountainous steppe and forest steppe areas of Southern Siberia and Mongolia.

The true Hermonassa species belong to an other tribe (Noctuini Kozhanchikov, 1937) and they have a short, broad vesica with a specialized dentate carina (Figs 40—44), which is often present in species of different Noctuini genera (e.g. Spaelotis Boisduval, Graphiphora Ochsenheimer, Paradiarsia McDunnough, Eugraphe Hübner, numerous Xestia Hübner species, etc.). The very uniform genus, rich in species, has a large number of taxa in the by monsoon influenced areas of Southern and South-Eastern Asia.

Three species, distributed mainly in Southern and Eastern Siberia and Mongolia, respectively, have a different external appearance and genital configuration, as compared with the true Hermonassa Walker species. One of them, "Hermonassa" melancholica Lederer, 1853 is mentioned in a manuscript of Boursin (List of the Palearctic Noctuidae, ined.) as Pseudohermonassa but this name has never been published. Because no valid name exists for "H." melancholica Lederer and the two related taxa (cicatricosa Graeser, 1892 = praecipua Staudinger, 1892; ononensis Bremer, 1864), we introduce here this 'in litteris' name with a short description.

Pseudohermonassa Varga gen. n.

Type species: Agrotis melancholica LEDERER, 1853 — Verh. zool.-bot. Ges. Wien, 367, t. 4, f. 3.

Diagnosis — medium-sized, relatively broad-winged, "Agrotis"-like moths, externally similar to some *Xestia* s. l. species. Frons convex, weakly sclerotized. Fore-tibiae longer than first tarsus.

Male genitalia (Figs 45—48): valvae short, apically acute; harpe short, broad, flattened. Vesica saccate, *P. melancholica* Lederer has a single, large, thorn-like, bulbed cornutus (as in some *Paradiarsia* species), this cornutus absent in *P. cicatricosa* Graeser and *P. ononensis* Bremer. Carina of these latter two species elongate, double, covered with teeth; in case of *P. melancholica* Lederer transformed into a dentate, sclerotized plate.

The new genus shows the closest relationship with *Paradiarsia* McDunnough (s. str.; type species: *litoralis* Packard, 1867); it contains the following species:

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melancholica (Lederer, 1853) (type species)
ononensis (Bremer, 1864) [= scaramangae (Alpheraky, 1892)]
cicatricosa (Graeser, 1892) [= praecipua (Staudinger, 1892)]
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The members of the new genus inhabit mainly the loose mountain taiga with large natural clearings in Southern and Eastern Siberia and Northern Mongolia, respectively.

4. Eugnorisma arenoflavida (Schawerda, 1936) bona species

For a long time the Iberian specimens of genus Eugnorisma Boursin, 1946 (except of the Pyrenean chain) were referred to Eugnorisma pontica (STAUDINGER, 1891), due to the external similarity between the two taxa due to certain resemblance in some genitalic features (see e.g. Agenjo 1941, 1977; CALLE 1983; and comments in VARGA et RONKAY 1987; YELA et SARTO in press; and FIBIGER in print). In the first part of their revision of genus Eugnorisma (VARGA et RONKAY, op. cit.), showed that the distribution area of Eugnorisma e.g. pontica extends from Greece to Iran (it is an East-Mediterranean species), and referred the Iberian specimens to Eugnorisma depuncta arenoflavida (Schawerda, 1934), pointing out that this supposed subspecies "very strongly differs in its appearance from the nominate depuncta LIN-NAEUS". In a preliminary approximation to the problem, the mentioned authors do not found consistant genitalic differences between the nominate depuncta LINNAEUS and arenoflavida Schawerda (the same ideas are expressed in FIBIGER, in print). After the study of large series of specimens of the two taxa of both sexes, significant and constant divergences were found

by the third author in vesica penis, distal lamina of the aedeagus and cervix and corpus bursae between both taxa. As the nominate depuncta LINNAEUS and arenoflavida were found at the same place in one locality of the Southern Pyrenean shore, the partial sympatry of the two taxa is evidenced; this fact supports the relegation of the latter one as a distinct species. This opinion has been confirmed by the discussion and second authors.

Material and methods — A large series of specimens of E. arenoflavida Schawerda of the Noctuidae collection of the Entomology Section of the M.N.C.N. (Museo National de Ciencias Naturales, Madrid), among them the type of the infrasubspecific form minaya Agenjo, 1941 (and therefore, according to the I.C.N.Z., a synonym of arenoflavida Schawerda), was examined. The whole material of the private collection of the third author (30 specimens of E. arenoflavida Schawerda and 12 of E. depuncta Linnaeus) was dissected and the genitalia were studied. Some specimens from other private and public collections (among them, the collections of the Instituto Alaves de la Naturaleza, Alava, and of the Sociedad Aranzadi, San Sebastian) were also studied.

The genital analysis method used by the third author was the habitual one, many times described in the literature for this type of studies. For everting vesicae penis and extending bursae copulatrix the method explained by LAFONTAINE & MIKKOLA (1987) was used.

Results — As pointed out in Varga et Ronkay (op. cit.) the external differences between E. depuncta and E. arenoflavida are conspicuous (see also plate 5, Figs 55 and 56 of Calle 1983). The following genitalic analysis made it that the genitalia (i.e. of the same general type) are very similar, as expected, but show a number of constant major and minor differences in its features, which could be briefly summarized as follows:

Male genitalia (Figs 22-23) - Major differences:

E. depuncta: diverticulum vesicae broader; dorsal sclerotized lamina at distal end of aedeagus more or less subrectangular, with 15—25 rows of dorsal and lateral spicules.

E. arenoflavida: diverticulum vesicae narrower; dorsal sclerotized lamina at distal end of aedeagus, shapened to its distal part, with 3—5 rows of dorsal spicules.

Minor differences:

E. depuncta: aedeagus longer and thinner, more curved; spinulose field of vesica more sclerotized and expanded; cornutus a bit shorter; valva more elongated; harpe broader and less curved; outer process of harpe longer and narrower.

E. arenoflavida: aedeagus shorter and broader, less curved; spinulose field of vesica lest sclerotized and expanded; cornutus a bit longer; valva shorter and heavily convexed in its central part, both in costal and anal margins; harpe narrower and more curved; outer process of harpe shorter and broader.

Female genitalia (Figs 24-25) Major differences:

E. depuncta: cervix bursae separated from corpus bursae very slightly; corpus bursae with a well-visible posterior lobe in front of cervix bursae.

E. arenoflavida: cervix bursae more prominent; posterior lobe of corpus bursae less developed.

Minor differences:

- E. depuncta: ostium bursae a bit broader; corpus bursae larger, longer and broader.
- E. arenoflavida: ostium bursae a bit narrower; corpus bursae not so large, shorter and narrower.

Discussion — In the preceding table "major differencis" mean differences in structures involved directly in the interaction, i.e. during copulation. The tip of the aedeagus and the proximal part of vesica with lamella antevaginalis, the ductus bursae and the posterior third of the corpus bursae (i.e. in "locking"), and the way of deposition and reception of the spermatophore may evidence mechanical isolation between the two taxa, and are therefore differences of specific level. "Minor differences" are divergences in structures with no direct usage in the mentioned copulatory mechanisms and therefore lacking of significance in the speciation process (secondary characters), or in structures involved directly in the mentioned mechanisms but less differentiated between the two taxa. The criteria for discriminating these characters are inferred from the "lock-and-key theory" (for Noctuidae, see e.g. Lafontaine et Mikkola op. cit., and bibliography cited there).

In spite of the observed differences, the genitalia of *E. depuncta* Linnaeus and *E. arenoflavida* Schawerda show a great number of similarities: unci, tegumina, fulturae inferiores, sacculi and vincula in the male genitalia and papillae anales, ostia bursarum and ducti bursarum in the female genitalia seem to be almost identical in both taxa. Vesica penis is also everted ventrally in both species, and its form may be called, using the term of Varga et Ronkay (op. cit.), horseshoe-shaped; although this is characteristic of all the *Metagnorisma* Varga et Ronkay, 1987 species.

The data taken by the third author from the labels of the examined material, the results of his personal captures and the bibliographical data shows that *E. depuncta* LINNAEUS lives only in the Pyrenean chain in the Iberian area, principally in warm slopes and more or less thermic valleys of the Central and Eastern Pyrenees. On the other hand, *E. arenoflavida* Schamerba is distributed widely throughout the Iberian Peninsula, much more than the map in Calle (1983: map 55) shows: it seems to be not very abundant, but it has been captured in localities from Galicia to the Basque Depression, in the Southern shore of the Navarran (Western) and Aragonian (Central) Pyrenees, in Portugal, in the whole Central Plateau and in the Betic and Penibetic Mountains (Andalusia). According to FIBIGER (in print), who considers *E. arenoflavida* Schawerda as subspecies of *E. depuncta* LINNAEUS, the former one lives in Morocco, too (see in Rungs 1981 as *E. "depuncta meridionalis* Danehl (sic!), 1925"). *E. arenoflavida* Schawerda is, then, an Atlanto-Mediterranean (West-Mediterranean) species.

E. arenoflavida Schawerda as subspecies of E. depuncta Linnaeus, the former one lives in Morocco, too (see in Rungs 1981 as E. "depuncta meridionalis Danehl (sic!), 1925"). E. arenoflavida Schawerda is, then, an Atlanto-Mediterranean (West-Mediterranean) species.

During the night of August, the 9th, 1984, one male of each of each species were captured by the third author at the same place: a 250 W mercury vapour lamp of the street lighting in a Southern Pyrenean valley (Valley of Eriste), in a town called Benasque (Huesca Province, Aragonia). This fact proves the partial sympatry of the two taxa and, as mentioned above, supports the consideration of E. arenoflavida Schawerda as a species distinct from E. de-

puncta Linnaeus.

Conclusions — Considering the constancy of the mentioned morphological differential characters in all the studied specimens and the partial sympatry, we can regard Eugnorisma arenoflavida (Schawerda, 1934) as a distinct species; having in mind the appointed morphological similarities, E. depuncta and E. arenoflavida could be considered two very closely related species resulting of a Pre-Pleistocenic splitting.

II. ZOOGEOGRAPHY

Although the present survey is based on the large materials of several important European collections, it is obvious, that the distribution of most Eugnorisma species is incompletely and unevenly known. The data are lacking from some Asian regions of zoogeographical importance. Only E. depuncta LINNAEUS has a wide, mostly European range of distribution; its sibling species, E. arenoflavida SCHAWERDA is confined to the central part of the Iberian peninsula and the Atlas Mts. (see the previous chapter). Other species of the genus display an irradiation only to Eastern or South-Eastern Europe. E. pontica Staudinger reaches its northwestern border at the southeastern gate of the Carpathian Basin, while E. caerulea WAGNER, E. chaldaica Bois-DUVAL, E. puengeleri VARGA et RONKAY and — last but not least — the generotype, E. insignata LEDERER occur only in the eastern steppe area of Southern Russia. All the species mentioned here have also a wide Central Asian-Southern Siberian distribution, principally in arid mountainous and steppe belts. Other species of wide distribution do not penetrate into the steppe areas, e.g. E. eminens LEDERER or E. trigonica Alpheraky. Numerous Eugnorisma species are strictly localized to some, mainly mountainous regions of Western or Central Asia. The apparent discontinuities in their distribution are originated only from our poor knowledge in some cases (e.g. E. rafidain Boursin, E. tamerlana Hampson, E. chaldaica Boisduval, E. variago Staudinger). However, the subspeciation of some stenochorous species (E. spodia PÜNGELER, E. deleasma Boursin, E. asad Boursin, etc.) suggests that some Eugnorisma species must have true disjunctions of evolutionary significance, too.

True stenochorous species seem to occur in (at least) three, fairly distinct regions. Eugnorisma asad Boursin, E. conformis Swinhoe, E. eucratides Boursin and E. goniophora Varga, Ronkay et Hacker sp. n. (see the description part) are restricted to the Western Transhimalayan mountains including E Afghanistan (countries of monsoonic influence!). Two of them belong to the E. insignata species-group — asad Boursin and conformis Swinhoe —, the two other consist of a pair of species, closely related to each other and perhaps to the hypothetical ancestors of the genus as well.

Some other stenochorous species are confined to the Tien Shan-Alai mountain system (including the Hissaro-Darwaz Mts.) with some irradiations

to the Hindukush and the W Pamir Mts.: E. deleasma Boursin (2 ssp.!), E. gaurax Püngeler (2 ssp.!), E. variago Staudinger (2 ssp.!). The third group contains the E Anatolian-Armenian-W Iranian species: E. enargiaris DRAUDT, E. rafidain BOURSIN and E. heuristica VARGA et RONKAY; all without any subspeciation. E. semiramis Boursin (SE Turkey, N Iraq + W Iran - "Kurdistan") and E. spodia PÜNGELER (Kopet Dagh + W Tien Shan) seem to be bicentric with geographic subspeciation.

Some further, very isolated species occur in Kashmir (E. fuscisigna HAMPSON), in Tibet (E. coryphaea PÜNGELER) and in W China (E. xestioides HAMPSON); each is taxonomically rather peculiar and isolated from other taxa of the genus.

On the basis of the distribution of the stenochorous species, we can state some types of distribution in Eugnorisma species, as follows (Figs 71-77):

1. Species with prevailing arboreal distribution.

1.1. Atlanto-Mediterranean: E. arenoflavida SCHAWERDA.

- 1.2. Ponto-Caspian (expansive): E. depuncta LINNAEUS; with Pre-Litorina exclaves in the British Isles and S Scandinavia.
 - 1.3. Ponto-Mediterranean (with peripheric subspeciation): E. pontica STAUDINGER.
 - 2. Species with prevailing non-arboreal (oreal and/or eremic) distribution.

2.1. E Anatolian (monocentric): E. enargiaris DRAUDT.

2.2. E Anatolian-Iranian (without subspeciation): E. rafidain Boursin, E. heuristica VARGA et RONKAY.

2.3. E Anatolian-Iranian (bicentric): E. semiramis Boursin.
2.4. E Anatolian-Iranian-Turkestanian (polycentric): E. caerulea Wagner (including ssp. kurdistana Hacker, Kuhna et Gross and ssp. isabellina Varga et Ronkay, with steppe exclaves), E. insignata LEDERER (including f. leuconeura, with steppe exclaves). E. eminens LEDERER (without steppe exclaves).

2.5. Turkmenian-Turkestanian (bicentric): E. spodia PÜNGELER. 2.6. Turkestanian (monocentric): E. chaldaica Boisduval (with steppe exclaves), E. puengeleri VARGA et RONKAY (with steppe exclaves), E. trigonica Alpheraky (purely xeromontane), E. tamerlana HAMPSON (mostly eremic).

2.7. Alai-Tien Shan-bicentric: E. variago Staudinger, E. gaurax Pungeler.

2.8. E Afghan: E. deleasma Boursin, E. atrabaelbops VARGA.

2.9. E Afghan-Transhimalayan: E. asad Boursin (bicentric), E. conformis SWINHOE, E. eucratides Boursin, E. goniophora Varga, Ronkay et Hacker.

From this outline we can conclude that

- the size of the area shows no close connection to the subspeciation (because the subspeciation is usually a consequence of the area regression refugial vs. peripheric isolation);
- two pairs of closely related species (E. depuncta LINNAEUS-E. arenoflavida Schawerda, E. gaurax Püngeler-E. deleasma Boursin) are strictly allopatric, since the sibling species are overlapping in two other cases (E. insignata Lederer-E. conformis Swinhoe, E. eminens Lederer-E. atrabaelbops VARGA); one of each pair is polycentric-expansive, the other one is stenochorous.

Some Eugnorisma species are abundant, in their habitats (e.g. E. caerulea WAGNER, E. insignata LEDERER, E. pontica STAUDINGER in E Turkey and Armenia; E. eminens LEDERER, E. insignata LEDERER and E. variago STAU- DINGER in NE Afghanistan: E. asad in NW Pakistan, etc.) but we known some species which never have been collected in great numbers (E. rafidain Boursin, E. atrabaelbops Varga, E. gaurax Püngeler, etc.). The most typical habitats of the Eugnorisma species are arid or semi-arid mountains with xerophytic vegetation, often covered with loose stands of scrub-like sclerophyllous forests (e.g. hard-leaved Ouercus, Juniperus, different Rosaceae, etc.).

III. PHYLOGENETIC CONSIDERATIONS

The genus Eugnorisma Boursin, 1946 was characterized in the original description and in some further papers (Boursin 1946, 1954) as closely related to Protexarnis McDunnough, 1929, based on the presence of a precostal lobe which must be homologous (sec. BOURSIN) with the 'digitus' of the Protexarnis species. In the first part of our revision we gave a more detailed redescription of the genus, from which only the following items are necessary to mention. Frons usually smooth, semiglobular, without any mark of a more sclerotized protuberance, like 'Triphaenini' genera sensu Kozhanchikov (1937). Fore tibiae are longer than the first joint of the tarsus; the claw-like appendix of the fore tibiae has nearly the same position as in Xestia (s. l.) or Paradiarsia (s. l.) species. In the male genitalia (Figs 49-70) the cucullus and the corona are usually reduced, the harpe is elongate, often falcate, the aedeagus is with a strongly sclerotized distal shield of the carina covered by tooth-like thorns or transformed into a hook-like emergence. The vesica is spatious, globular, semiglobular or saccate, with a proximal or medial diverticulum, terminated in a spine-like, not bulbed cornutus. The females of the Eugnorisma species usually have a strongly sclerotized ostium and ductus bursae, the latter is folded or plicate. All these features contradict the taxonomic relegation suggested by Boursin. The genus Protexarnis is closely allied to Parexarnis Boursin, 1946 and to some other genera (e.g. Ledereragrotis gen. n. for multifida LEDERER and difficilis ERSHOV; Hemiexarnis BOURSIN and Dichagyris LEDERER s. l.). It means, that Protexarnis belongs to the tribe Agrotini sensu KOZHANCHIKOV (versus Franclement et Todd 1983) and the reduction of the corona may be only a convergent character. Protexarnis species usually have a long, tubular vesica with helicoid coiling; the ostium and the ductus bursae are less sclerotized, the bursa is bilobate (as in Parexarnis, Dichagyris, etc.). All these facts confirm our opinion that the genera Eugnorisma and Protexarnis (and Hemiexarnis, Parexarnis, etc.) cannot be closely related to each other.

In order to the correct phylogenetic relegation of the genus *Eugnorisma* we have to analyze all features, mentioned in the characterization of the genus. Some of them (e.g. the smooth frons, the reduced cucullus and corona and the number of rows of the spines on the tibiae and tarsi) do not have any

phylogenetic significance because of their convergential appearance in numerous genera of Noctuinae. We have already pointed out that the uniform configuration of the vesica, the shield-like sclerotized plate of the carina and the heavily sclerotized ostium and ductus bursae are the mean indications supporting the phylogenetic coherence of the genus. At the same time these features suggest the more close relationship to the genera Eugraphe HÜBNER, 1821, Paradiarsia McDunnough, 1929, and, at all, to the Xestia-complex. All these genera have globular or saccate vesica which is strengthened at the sinus penis by one (or two) dentated crest(s). We think that the sclerotized shield of the carina in the Eugnorisma species can be derived from this structure and, therefore, it can be considered as a synapomorphic feature for all Eugnorisma species. The presence of a lateral pollex is a common character of numerous Xestia s. l., Paramathes Boursin, Eugraphe and Paradiarsia s. l. species the heterogeneity of the genus Paradiarsia is an obvious fact but this problem can be solved only in the scope of a Holarctic revision), however it can disappear in some species and/or species groups, as a convergent reduction (see subg. Metagnorisma VARGA et RONKAY, 1987, Eugraphe (Hypernaenia) denticulata WARREN, Ammogrotis suavis STAUDINGER, Paradiarsia litoralis PACKARD, 'Paradiarsia' sobrina BOISDUVAL, etc.). The reduction of the lateral diverticulum and cornutus can be observed in some Paradiarsia and in the most Xestia species, and — within the genus Eugnorisma — in two distinct species, E. enargiaris DRAUDT and E. semiramis BOURSIN. The spinulose field near to the ductus ejaculatorius occurs regularly in Eugnorisma species. It can serve as a distinctive feature as opposed to Eugrapha, Paradiarsia, Paramathes, Xestia, etc. However, it is difficult to decide, whether its missing in two, closely related Eugnorisma species (E. eucratides Boursin and E. goniophora VARGA. RONKAY et HACKER) is a result of a reduction or it is a primary common feature with the related genera. The transformation of the granulous structure of the vesica into such a spinulose field shows hardly any well-defined phylogenetic trend; it may appear and disappear in other, not closely related groups (e.g. Parexarnis, Protexarnis), too. Therefore, the exact sister-group relationships of the mentioned genera can be analyzed only within a complete revision of the tribe Noctuini. Presumably, Eugraphe (or at least one species group within Eugraphe) may be the closest relative of Eugnorisma, but some species of the small, heterogeneous genus Paramathes Boursin, 1954 (e.g. P. tibetica Boursin, P. perigrapha Püngeler) also have to be taken into consideration.

The relations within the genus Eugnorisma are far less confused. Only one species is difficult to be judge because of the lack of the male, E. coryphaea PÜNGELER. Two species seem to form a special group, missing the spinulose field of the vesica. Based on the position and shape of the cornutus, we think

that E. xestioides Hampson must be their closest relative. The subgenus Metagnorisma described in the first part forms an other compact, well-defined group within the genus. Because they have three important synapomorphies with the other species of the genus Eugnorisma (the globular vesica with the spinulose field and the dentated lamina of the carina) we cannot separate it on generic level. The reduction of the pollex can be regarded as an autapomorphy of this subgenus, its role is seemingly adopted by the strongly sclerotized base of the harpe which is relatively short and broad. Other two features: the presence of signa and the less sclerotized ostium bursae seem to be rather plesiomorphic ones, disappeared in other Eugnorisma species.

Another important apomorphic feature of the genus is the pollex covered by scale-like macrotricha, being characteristic of two species groups (insignata-and trigonica-group). The very long, falcate harpe and the strong, spinulose shield of the carina are the synapomorphies of the species E. chaldaica, E. puengeleri and E. tamerlana; since the hook-like transformation of this shield seems to be apomorphic for the spodia-caerulea species-pair. The disappearance of the large diverticulum and the cornutus in E. enargiaris and E. semiramis — as they are very dissimilar in all other features — must be only an accidental congruence.

All the mentioned characteristics are considered in the cladogram (Fig. 78) from which two species are omitted: *E. fuscisigna* Hampson (because we had no opportunity to study any specimen) and *E. coryphaea* PÜNGELER (because its taxonomic relegation is uncertain as the male is unknown).

The Eugraphe species differ from Eugnorisma in some essential points: they have a bulbed cornutus sitting usually on a very short diverticulum (or missing, see E. ornata STAUDINGER) and the high, narrow tegumen. As the peculiar species, miniago FREYER shows both of these features but nothing from the Eugnorisma-apomorphies, we consider it as a modified member of the genus Eugraphe. Furthermore, 'Eugraphe' suavis STAUDINGER must be excluded from this genus because it has elongate and acute valvae without any pollex, the harpe is very short and thick and it has a fairly typical clavus (as a plesiomorphic character). In addition, the moth has a somewhat curious external appearance. Therefore we suggest the restitution of the original, often misidentified (KOZHANCHIKOV 1937) genus, Ammogrotis STAUDINGER, 1895, which contains only this single known species.

Spatio-temporal aspects of the evolution in Eugnorisma — The phylogenetically oldest members of the genus are strictly localized, relict-like species, occurring in some isolated mountainous regions of E-SE Asia having more or less intensive monsoonic influence. They are presumable reductional relicts (UDVARDY 1969) and their former distribution is confuse. Some other, also relict-like stenochorous species occur in E Anato-

lia-Armenia and Central Asia, respectively. However, they are relic species only in a zoogeographical sense, because they can be characterized by some (partly convergently derived) characters as the lack of the cornutus in *E. enargiaris* and *E. semiramis*, the appearance of a pale yellowish ground colour versus the greyish one in *E. heuristica*, *E. enargiaris*, *E. variago*, etc.

Some of the stenochorous species reach a NW border of their distribution at the more cold-continental mountains of N and E Afghanistan, e.g. E. conformis and E. asad does not occur either in the main chain of the Hindukush Mts. or in the NE (Badakhshan) edge of the country (Mts. Darwaz and the Pamir). At the same time, some expansive members of the genus, which are distributed widely in the arid continental Central Asiatic Mts. (E. insignata, E. eminens, E. puengeleri) are able to reach the mountains of E Afghanistan (Nuristan) and NW Pakistan, too. Other species have a southern limit in the cold-continental NE Pamir and the Hissaro-Darwaz region (E. deleasma, E. variago). Others do not occur southwards from the Alai and W Tien Shan Mts (E. spodia psammochrea, E. gaurax, E. chaldaica). From the Central Asiatic species only E. tamerlana shows an adaptation to desert habitats (in Transcaspia, Turkmenia and Uzhbekistan).

The evolution and distribution of the species groups having macrotricha on the pollex has particular importance. It seems that this group also differentiated in the semi-arid mountains of Central Asia, perhaps mostly in the W Tien Shan, where special types of xerophilous broad-leaved forests grow ('apple-forests'). One part of these species - the trigonica group - remained only in the arid - semi-arid high mountains. The distribution of the more recently dispersed, 'successful' species, E. trigonica covers nearly exactly the entire area of the purely allopatric species-pair E. gaurax-E. deleasma. The latter two show a marked tendency for evolving into geographically isolated endemic races: E. deleasma reducta — E Hindukush, E. deleasma hissarica - Hissaro-Darwaz Mts., E. deleasma deleasma - Pamir; E. gaurax gaurax - W Tien Shan, E. gaurax funebris - Alai Mts. The other part of the species - the insignata group - is more vigorously differentiated; one species is also widely distributed in the steppe areas (E. insignata). The most conspicuous species of this group, E. semiramis, shows a western, localized (disjunct?) distribution in the "Kurdistan" triangle of Turkey, Iraq and W Iran and Farsistan (Iran), respectively. Its genital configuration suggests that the subgenus Metagnorisma can be derived from a similar but more ancient western wave of dispersal, passing an important biogeographical filter during the Neogene (Upper Miocene) xerophilization of the Eastern Mediterranean vegetation. These Metagnorisma species show reductional tendencies in the male genitalia and connected to some (semi-open) xeric arboreal habitats. It seems to be evident that their dispersal into the W Palaearctic and their connection to (at least partly) xerophilous forest or scrub-forest habitats depends closely

on each other. The species, witnesses of the more ancient speciation wave of this subgenus, are obviously relict-like ones (E. arenoflavida in SW Europe and NW Africa, E. heuristica and E. rafidain in Asia Minor). The more continuous, Ponto-Mediterranean distribution of E. pontica with peripheric subspeciation in the Armenian plateau, W Iran and Transcaspia may be a more recent (Upper Pleistocene and postglacial) phenomenon; similarly to the formation of the nearly continuous European range of E. depuncta from a Ponto-Caspian arboreal center. The expansion of E. depuncta must have taken place before the Litorina transgression, because the species could reach the British Isles and S Scandinavia before the major Holocene re-forestation and the expansion of the humid, closed, broad-leaved forests of Carpino-Fagetea which have begun in the Atlanticum. E. arenoflavida is surely not a peripheric isolate of this very young postglacial expansion but a relict species, an early stage of the evolution of the subgenus, lacking the connection to the Eastern Mediterranean relatives.

The occurrence of some C Asiatic—South Siberian species at the easternmost steppe belts of Europe can be regarded as an other recent distributional phenomenon, connected to the postglacial history of the zonal steppe biome. It is supported by the fact that one can observe no subspeciation in these cases. On the other hand, it is a well-known phenomenon, that zonally distributed plant and animal species of the E-SE steppe zone can be derived from relatives inhabiting the mountainous steppe (xeromontane) habitats of the vast Central-Asiatic Mts. (VARGA, 1975, 1989).

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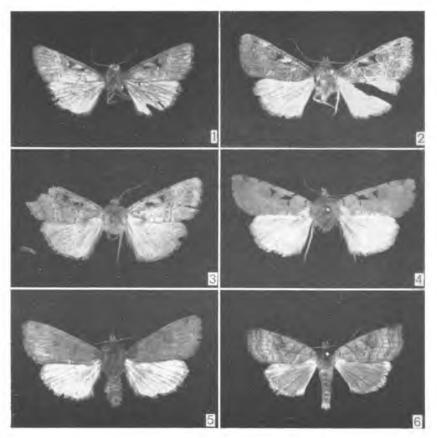
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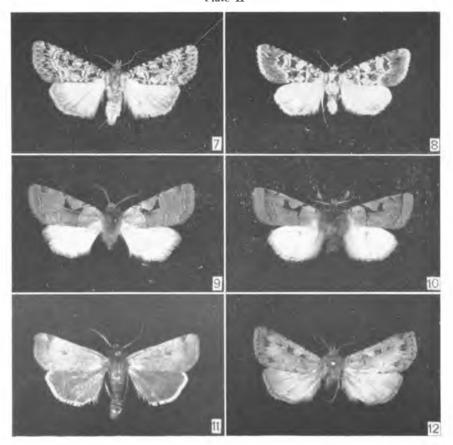
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Plate I

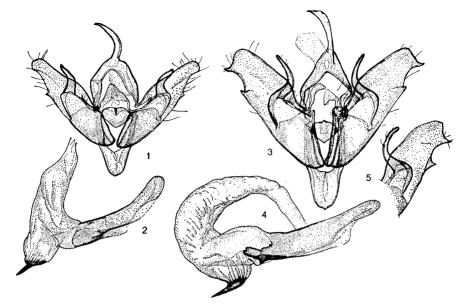


1. Eugnorisma goniophora sp. n. Holotype, Pakistan. 2. Eugnorisma goniophora sp. n. Paratype, Pakistan. 3. Eugnorisma eucratides Boursin: Afghanistan, Nuristan. 4. Eugnorisma caerulea rubicunda ssp. n. Paratype, Sibiria. 5. Eugnorisma asad plantei ssp. n. Paratype, Pakistan, Babusar Pass. 6. Eugnorisma xestioides Hampson: China, N Yuennan.

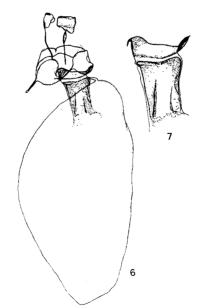
Plate II



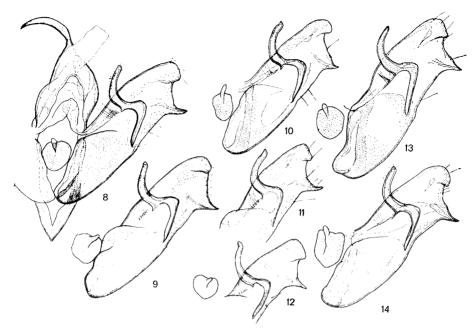
7. Eugraphe funkei Staudinger: Afghanistan. 8. Eugraphe ornata Staudinger: Afghanistan. 9. Paleamathes tibetica Boursin: China, Richthofen Mts. 10. 'Paramathes' picata Bang-Haas: Algeria. 11. Paradiarsia litoralis Packard: Canada. 12. Xestia (Anomogyna?) coelebs Staudinger: China, Tibet (Kuku-Noor).



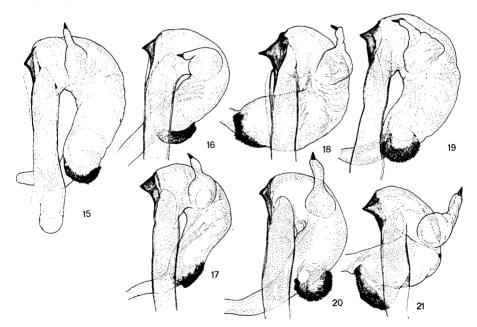
Figs 1—5. 1—2 = Eugnorisma goniophora sp. n. Holotype, Pakistan, 3—5 = Eugnorisma eucratides Boursin: 3—4 = Afghanistan, Nuristan, 5 = Paghman.



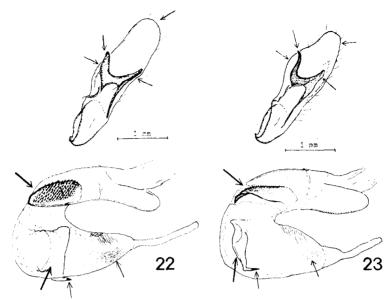
Figs 6-7. Eugnorisma goniophora sp. n. Paratype, Pakistan.



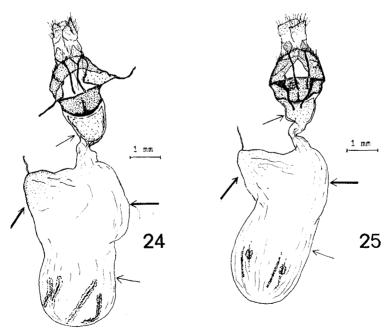
Figs 8—14. 8—10 = Eugnorisma caerulea Wagner: 8 = paratype, Turkey, 9 = Turkey, Erzurum, 10 = Armenia, Geghard. 11—12 = E. caerulea rubicunda ssp. n. 11 = holotype, Margelan, 12 = paratype, Altai. 13 = E. caerulea kurdistana Hacker, Kuhna et Gross: paratype, Turkey. 14 = E. caerulea isabellina Varga et Ronkay: paratype, Iran.



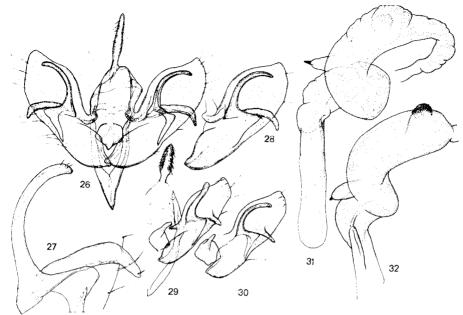
Figs 15—21. 15—17 = Eugnorisma caerulea Wagner: 15 = paratype, Turkey, 16 = Turkey, Erzurum, 17 = Armenia, Geghard. 18 = E. caerulea kurdistana Hacker, Kuhna et Gross: paratype, Turkey E. 19 = E. caerulea isabellina Varga et Ronkay: paratype, Iran. 20—21 = E. caerulea rubicunda ssp. n.: 20 = paratype, Altai, 21 = holotype, Margelan.



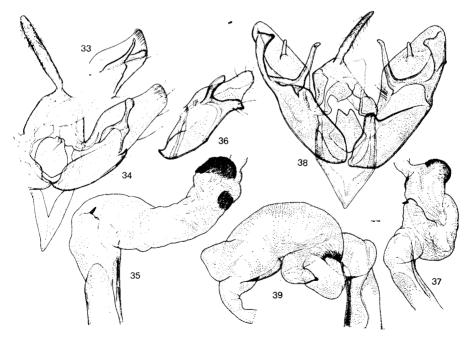
Figs 22-23. 22 = Eugnorisma (Metagnorisma) depuncta Linnaeus: Spain. 23 = E. (M). arenoflavida Schawerda: Spain.



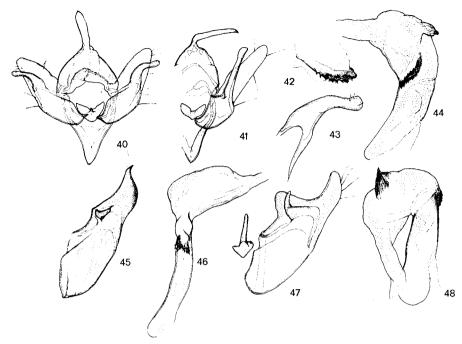
Figs 24—25. 24 = Eugnorisma (Metagnorisma) depuncta Linnaeus: Spain. 25 = E. (M.) aren flavida Schawerda: Spain.



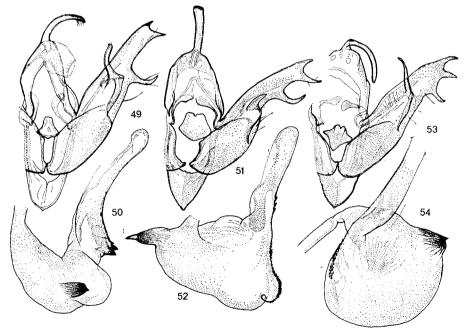
Figs 26-32. 26—28 and 31. Ledereragrotis multifida Lederer: 26—27 = Alpes, 28 and 31 = Caucasus. 29—30 and 32 = L. difficilis Ershov: Mongolia.



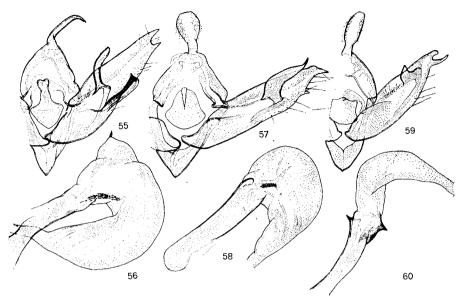
Figs 33—39. 33 = Dichagyris grisescens Staudinger: holotype. 34—35 = Parexarnis damnata Boursin: Iran. 36—37 = Protexarnis monogramma Hampson: Afghanistan, Badakhshan. 38—39 = Protexarnis squalida Guenée: Mongolia.



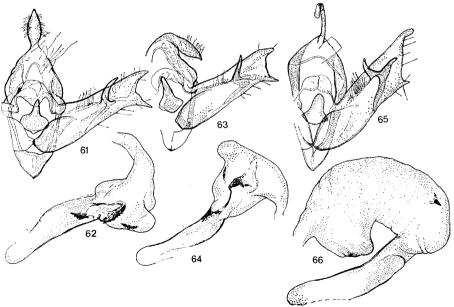
Figs 40-48. 40 and 42-43 = Hermonassa consignata WALKER: Nepal. 41 and 44 = H. stigmatica WARREN: Nepal. 45 = 46 = Pseudohermonassa cicatricosa GRAESER: Mongolia. 47-48 = P. melancholica Lederer: Mongolia.



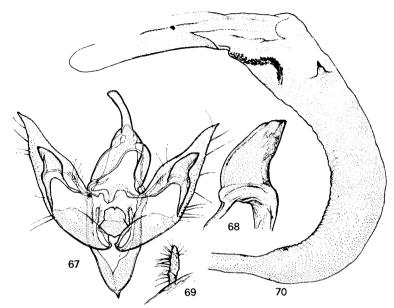
Figs 49—54. 49—50 = Eugraphe funkei Staudinger: Afghanistan. 51—52 = E. decussa Staudinger: Afghanistan. 53—54 = E. marcida Christoph: Turkestan.



Figs 55—60. 55—56 = 'Paramathes' picata Bang-Haas: Algeria. 57—58 = Palaeamathes tibetica Boursin: China, Richthofen Mts. 59—60 = Xestia (Anomogyna?) coelebs Staudinger: China, Kuku-Noor.



Figs 61—66. 61—64 = Xestia (?Pachnobia) senescens STAUDINGER: 61—62 = Tien Shan, 63—64 = Kuldja. 65—66 = 'Opigena' albifurca Ershov: Mongolia.



Figs 67-70. Ammogrotis suavis STAUDINGER: Mongolia.

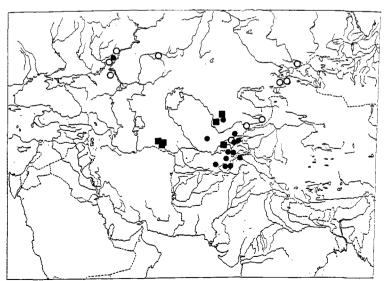


Fig. 71. Distribution of E. tamerlana HAMPSON (dark quadrate), E. chaldaica Boisduval (empty circle) and E. puengeleri Varga et Ronkay (full circle).

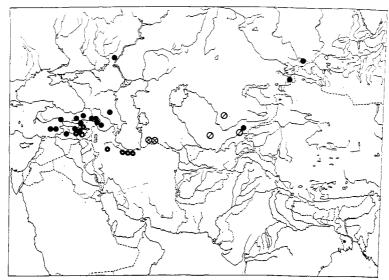


Fig. 72. Distribution of E. spodia Püngeler (large circles; the two subspecies with different marks) and E. caerulea Wagner (small circles; the sspp. kurdestana Hagner, Kuhna et Gross and isabellina Varga et Ronkay with white centre).

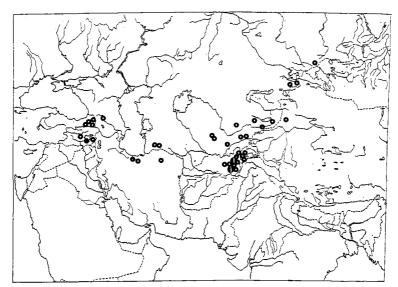


Fig. 73. Distribution of E. eminens LEDERER (small circle) and E. atrabaelbops VARGA (large circle with transverse bar).

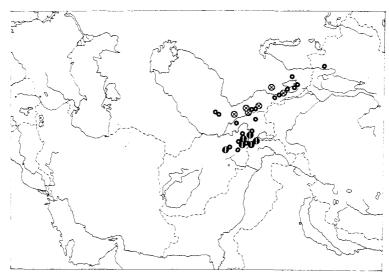


Fig. 74. Distribution of E. trigonica Alpheraky (small circles), E. gaurax Püngeler (large circles with X-mark) and E. deleasma Boursin (large circles with white bar).

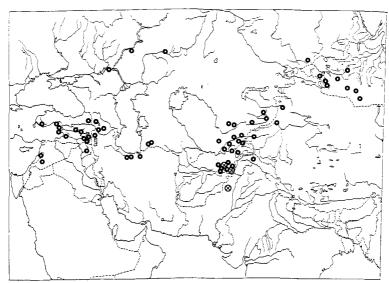


Fig. 75. Distribution of E. insignata LEDERER (small circles) and E. conformis SWINHOE (large circles with X-mark).

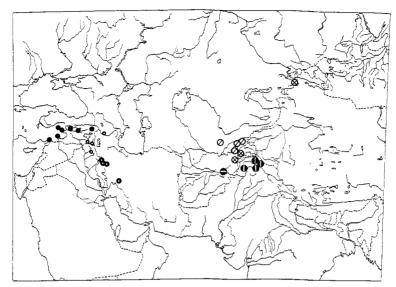


Fig. 76. Distribution of *E. enargiaris* Draudt (full circles), *E. semiramis* Boursin (nominate race marked with small circles, ssp. *farsica* Boursin with medium circles with white centres), *E. variago* Staudinger (large circles with X or /-marks) and *E. asad* Boursin (large circles with white transversal or longitudinal bars).

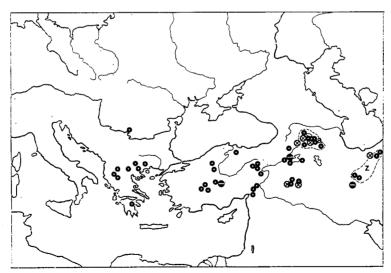


Fig. 77. Distribution of E. (M.) pontica Staudinger (small circles), E. rafidain Boursin (large circles with white bars) and E. heuristica Varga et Ronkay (large circles with X-mark).

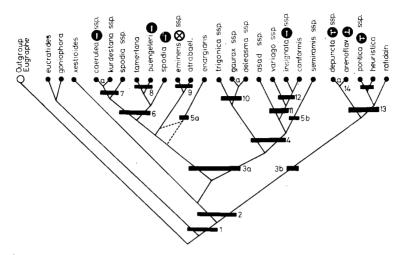


Fig. 78. The cladogram of the Eugnorisma species (the synapomorphies indicated by numbers and markings are as follows: 1 = diverticulum with strong cornutus, heavily sclerotized ostium and ductus bursae; 2 = spinulose field of vesica present; 3a, 3b- signum absent versus signum present, apex bursae rugulose versus apex bursae membranous; 4 = pollex covered with macrotricha; 5a, 5b = reduction of cornutus; 6 = characteristic wing pattern; 7 = hook-like sclerotization of carina; 8 = elongate valvae with falcate harpe; 9 = characteristic black pattern of forewings; 10 = characteristic, 'trigonic' black markings; 11 = vesica broad, saccate, diverticulum long and curved, ostium bursae broad, triangular; 12 = apex bursae conical; 13 = reduction of pollex; 14 = valvae broad and rounded. a = allopatric pairs of species; circle with X-mark- expansive species with penetrance to steppe belt; circle with bifid arrow-mark- expansive species with penetrance to steppe belt; circle with bifid arrow-mark- expansive species with penetrance to steppe belt; circle with bifid arrow-mark- expansive species with penetrance to phil-mesophilous arboreal zone).