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# NEUE ENTOMOLOGISCHE NACHRICHTEN

aus dem Entomologischen Museum  
Dr. Ulf Eitschberger

Beiträge zur Ökologie, Faunistik  
und Systematik von Lepidopteren

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ZSOLT BÁLINT & KURT JOHNSON

Reformation of the *Polyommatus* Section  
with a Taxonomic and Biogeographic Overview  
(Lepidoptera, Lycaenidae, Polyommataini)

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# Reformation of the *Polyommatus* Section with a Taxonomic and Biogeographic Overview

(Lepidoptera, Lycaenidae, Polyommagini)

by

ZSOLT BÁLINT & KURT JOHNSON

„Es ist der Wurf des Säemanns, wenn er fasst  
Mit der Schaufel den Weizen,  
Und wirft, den Klaren zu, ihn schwingend über die Tenne.  
Ihm fällt die Schale vor den Füßen, aber  
Ans Ende kommet das Korn,  
Und nicht ein Übel ist, wenn einiges,  
Verloren gehet und von der Rede  
Verhallet der lebendige Laut,  
Denn göttliches Werk auch gleicht dem unsern,  
Nicht alles will des Höchste zumal.“  
F. HÖLDERLIN, Patmos [1802]

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## Dedication

The late CHARLES A. BRIDGES, at the time of his revising BRIDGES (1988), requested the authors' aid in more fully elaborating the composition of the *Polyommatus Section* of the Tribe Polyommatini. At the time, significant work on these groups was *in press* and it was not possible to make all of it available for examination. Nonetheless, BRIDGES included many changes based on correspondence with the present authors (BRIDGES, 1994). The revision of the *Polyommatus Section* which follows below confirms, or further elaborates upon, many of the original queries of BRIDGES. Accordingly, we dedicate this study of the *Polyommatus Section* to his memory.

## Abstract

The generic composition of the *Polyommatus Section* of the Polyommatini, originally proposed by ELIOT mostly from studies of male genitalia and including 33 valid generic names, is revised.

Recent revisionary works, including study of morphological (and other) characters in both sexes indicates the following genera must be excluded: *Cyclargus* NABOKOV, 1945; *Echinargus* NABOKOV, 1945; *Hemiargus* HÜBNER, [1819]; *Itylos* DRAUDT, 1921 (= *Parachilades* NABOKOV, 1945); *Nabokovia* HEMMING, 1960 and *Pseudochrysops* NABOKOV, 1945.

Characters are reviewed for the nine genera remaining in *Polyommatus Section*:

*Agriades* HÜBNER, [1819];

*Albulina* TUTT, 1909 (= *Farsia* ZHDANKO, 1992, **syn. nov.**; *Pamiria* ZHDANKO, 1994, **syn. nov.**; *Patricius*

BÁLINT, 1991, **syn. nov.** and *Plebejidea* KOÇAK, 1993, **syn. nov.**);

*Aricia* [REICHENBACH], 1819 (= *Umpria* ZHDANKO, 1994, **syn. nov.**);

*Chilades* MOORE, [1881] (= *Lachides* NEKRUTENKO, 1984, **syn. nov.**);

*Madeleinea* BÁLINT, 1993;

*Paralycaeides* NABOKOV, 1945;

*Plebejus* KLUK, 1802 (= *Alpherakya* ZHDANKO 1994, **syn. nov.**);

*Polyommatus* LATREILLE, 1804 (= *Elviria* ZHDANKO, 1994, **syn. nov.**) and

*Pseudolucia* NABOKOV, 1945.

A list of genera and species is given. Three replacement names are proposed:

*Plebejus ardis* BÁLINT & JOHNSON, **nom. nov.** (replaces *Lycaena eversmanni* STAUDINGER, 1894),

*Plebejus beani* BÁLINT & JOHNSON, **nom. nov.** (replaces *Lycaena indica* EVANS, 1925) and

*Plebejus pilgram* BÁLINT & JOHNSON, **nom. nov.** (replaces *Lycaena serica* GRUM-GRSHIMAILO, 1902).

From examination of type material, the following new species level synonymies are established:

*Aricia monarchus* HIGGINS, 1981 (**junior synonym** of *Papilio semiargus* ROTTEMBERG, 1775),

*Lycaena idas tshimgana* FORSTER, 1936 (**junior synonym** of *Lycaena argus* f. *naruenta* COURVOISIER, 1913),

*Plebejus balinti* D'ABRERA, 1993 (**junior synonym** of *Lycaena buddhista* ALPHERAKY, 1881),

*Polyommatus tibetanus* FORSTER, 1940 (**junior synonym** of *Polyommatus annulatus* ELWES, 1906)

and *Vacciniina Iornex* HIGGINS, 1981 (**junior synonym** of *Plebejus lucifera selengensis* FORSTER, 1940).

A hypothetical branching diagram of the *Polyommatus Section* is presented and discussed, with notes concerning historical context (especially regarding the Plebejinae system of NABOKOV). The phenomenon of wing discoloration in certain Polyommatini is discussed in light of new data concerning geographic distribution and apparent endemism in various of these taxa. Also examined are historical and current methods of studying the Polyommatini and various views of the tribes's overall diversity.

In an Appendix, six polyommatine lycaenids are described: *Agriades kurtjohnsoni* BÁLINT, **spec. nov.** from Nepal, *Albulina gaborronkayi* BÁLINT, **spec. nov.** also from Nepal, *Polyommatus frauartiana* **spec. nov.** from Afghanistan, *Polyommatus fabiani* **spec. nov.** from Mongolia, *Polyommatus delessei* **spec. nov.** from Iran and *Madeleinea gradoslamasi* **spec. nov.** from Peru.

## Introduction

ELIOT (1973), in his higher classification of the Lycaenidae, proposed the *Polyommatus Section*.<sup>1</sup> It was actually identical with NABOKOV's polyommatine subfamily Plebejinae (NABOKOV, 1945). As recent work has pointed out, ELIOT's *Polyommatus Section* was polyphyletic (sensu NELSON 1971) (BÁLINT & JOHNSON, 1995a, b, c; JOHNSON & BÁLINT 1995). A number of factors contributed to this. Firstly, ELIOT's review (which was titled as a "tentative" study of the family) was (1) limited to the study of males of selected taxa representing the many generic names available in the family, (2) did not attempt to evaluate species statuses or, therefore, primarily consult type material. Secondly, as ELIOT has recently pointed out (in litt. to JOHNSON, 1996), he was aware of the sampling error problem in the New World fauna and, primarily as a specialist in the Oriental Realm, assumed his cursory approach to the New World would eventually lead to followup work by others.

ELIOT (1973: 450) listed 33 genera in his *Polyommatus Section*. Recent revisionary works (see literature cited in BÁLINT & JOHNSON, 1995a: 220) have included study of far wider arrays of taxonomic characters, including not only wing structure and pattern but genitalia and tergal morphology in both sexes; such studies have included virtually all known taxa of the Polyommataini in the New World. These studies have demonstrated that ELIOT's original *Polyommatus Section* was polyphyletic and indicate that the following Neotropical genera (as listed by ELIOT) must be excluded from that section: *Hemiargus* HÜBNER, [1819]; *Pseudochrysops* NABOKOV, 1945; *Cyclargus* NABOKOV, 1945; *Echinargus* NABOKOV, 1945; *Nabokovia* HEMMING, 1960 and *Itylos* DRAUDT, 1921 (= *Parachilades* NABOKOV, 1945).

The genera remaining in the section compose a "reformed" *Polyommatus Section*. This term was originally employed by BÁLINT & JOHNSON (1995a, c). Since their studies included only detailed treatment of Neotropical components, the purpose of the present paper (based primarily on adding Holarctic data produced by the senior author) is to review the "reformed" *Polyommatus Section* worldwide and thus establish this view of the section as normative. As reconstituted, the *Polyommatus Section* appears to be the sister group of the pan-American *Nabokovia Section*, which includes two Neotropical genera, *Echinargus* NABOKOV, 1945 and *Nabokovia* HEMMING, 1960 (see Discussion below).

In the following entries, we briefly characterize all the genera of the *Polyommatus Section* as now understood. Each one constitutes a distinctive morphological, biogeographical, and biological entity.

## Material and methods

The results of the present paper are based on (1) studies of historical type material and specimens housed primarily in the large European collections rich in historical polyommatine lycaenid materials and (2) historical and recent material acquired from the neotropics as outlined in BÁLINT & JOHNSON (1995a). The Natural History Museum (BMNH, London, United Kingdom), Museum Nationale d'Histoire Naturelle (MNHN, Paris, France) and Zoologische Staatssammlung (ZSM, Munich, Germany)

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1 The term "section" is somewhat misleading because of the official systematic term "sectio" The ELIOTian section means, practically, genus-group. To be compatible with one of the most important works ever published on lycaenid systematics, we apply the term of ELIOT.

were visited several times and provisional polyommata checklists prepared. Important unelaborated Neotropical lycaenid samples were received for study from the American Natural History Museum (AMNH, New York, USA) and FIELD Museum of Natural History (FMNH, Chicago, USA), and collections were examined by both authors at The Natural History Museum (BÁLINT, 1993a, b) and by the senior author at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM, Lima, Peru). Specimens were also provided by the late Señor LUIS PEÑA and Mr. DUBI BENYAMINI from Argentina, high Andean Bolivia, and Chile (see historical comments in BÁLINT & JOHNSON 1995a:215–216).

More than 700 male and female genitalic dissections were made by the senior author (most maintained in catalogued vials and slides at the Hungarian Natural History Museum (HNHM) as gen. prep. Nos 1–758, BÁLINT). An additional survey of some 200 genitalia by the junior author, representing AMNH, FMNH and PEÑA samples, is maintained in microvials returned with specimens to these respective collections. These data were compared to over 500 historical figures (most important sources: FERNANDEZ-RUBIO, 1976; HIGGINS, 1975; NEKRUTENKO, 1985; STEMPFFER, 1937 and 1967 and additional slides or vial materials at the museums visited) primarily during comparative work by the senior author from 1995–1996.

Below, under the subtitle “Generic Classification of the Reformed *Polyommatus Section*” all pertinent genera are listed in alphabetic order and, thereafter, characterized.

A taxonomic list (Species Diversity of the *Polyommatus Section*), including the generic and species levels, is provided. This list omits subspecies, which require revisionary work within the individual species groups (or “subgenera”, see below). The geographic distributions for all hierarchical taxonomic levels are briefly summarized with the help of generalized geographic terms. Entries summarizing geographic distribution start with the capital letters of main biogeographical regions where groups occur. The major abbreviations are listed on Table 1.

Table 1

Abbreviations referring to the traditional biotic realms or regions used under Species Diversity of the *Polyommatus Section*

abbreviation	region
AFR	Afrotropics
NA	Nearctic
NT	Neotropics
OR	Oriental
PA	Palaearctic
HA	Holarctic (given only in a few cases)

Subsequent citations of more detailed, or biogeographically more informative, distributions, follow the authors' judgements of heuristic value. For example, if distributions are catholic throughout major regions, generalized terms like “Eurasia” (all of Europe and Asia) are used. If distributions are more disjunct within major regions, citations like “PA: C Asia and W Himalayas” are employed. For some larger taxonomic groupings, broad distributions coincident with areas of tectonic significance are noted. For example, if a distribution includes all the elements of the supercontinent Laurasia, “Laurasia” may be mentioned; if a distribution is distinctly east Asian and adjacent Alaska, “Berigian” may be listed.

In regard to terminology, forewing lengths refer to alar expanse (base to wingtip); for brevity these are noted as “FW length”. Use of the term “usual polyommata pattern” refers to the “catochrysoptoid” wing pattern as generalized by NABOKOV (1945); use of the word “extended” with regard to this pattern refers to the distension of pattern elements within the intercellular spaces common to many polyommata species. Morphological terminology follows that initiated by NABOKOV (1945) and subsequently employed in recent works of the present authors cited herein.

Interrelationships of the genera are considered in the Discussion and a hypothetical branching diagram is presented based on inferences concerning polarity of characters within the section following ELIOT who considered the more sclerotized structures, and those without additional components, to be generally primitive (ELIOT, 1973: 382–409).

## Results

### Generic Classification of the Reformed *Polyommatus* Section (hereafter, the “*Polyommatus* Section”)

The genus *Agríades* HÜBNER, [1819] (figs. 9, 10)

Diagnosis – Wings: Generally small butterflies (FW length generally less than 2 cm), hindwing without tails; male ground colour greenish or bluish often with bronze suffusion, females generally brown. Hindwing ventrum with extended white elements around usual polyommataine pattern. Genitalia: Male genital aedeagus short and stout, typified by short suprazonal element with more or less parallel lateral edges and membranous extension. Female genital ductus bursae evertable but also short and strong, tubelike in shape with sclerotized basal plate at terminus.

Distribution – Holarctic.

The genus *Albulina* TUTT, 1909 (figs. 19, 20)

Diagnosis – Wings: Generally medium sized polyommataines (FW length between 2 and 3 cm), hindwing without tails; male ground colour blue, females generally brown. Hindwing with usual polyommataine pattern reduced but marked with extended white. Genitalia: Male genital aedeagus relatively elongate and showing a suprazonal element with lateral edges more or less parallel and a membranous extension. Female genital ductus bursae elongate and evertable and with a sclerotized basal plate at the terminus.

Distribution – Holarctic.

Taxonomy – The following taxa, previously regarded as valid genera or subgenera can be considered as synonyms of *Albulina*; listed in alphabetical order: *Farsia* ZHDANKO, 1992; *Pamiria* ZHDANKO, 1994; *Patricius* BÁLINT, 1991; *Plebejidea* KOÇAK, 1983 and *Vacciniina* TUTT, 1909, all **syn. nov.**

The genus *Aricia* [REICHENBACH], 1817 (figs. 7, 8)

Diagnosis – Wings: Small or medium sized polyommataines (FW length generally between 1.8–3 cm), hindwing without tails; male ground colour greenish or, more often, bluish, females generally brown. Hindwing ventrum with usual polyommataine pattern extended. Genitalia: Male genital aedeagus with pointed suprazonal element generally longer than subzonal, slightly curved in lateral view. Female genital ductus bursae long and evertable with terminal tube and sclerotized structures.

Distribution – Holarctic.

Taxonomy – The following taxa previously regarded as valid genera or subgenera can be considered as synonyms of *Aricia*; listed in alphabetical order: *Eumedonia* FORSTER, 1938; *Icaricia* NABOKOV, 1945; *Pseudaricia* BEURET, 1959; *Ultraaricia* BEURET, 1959 and *Umpria* ZHDANKO, 1994, all **syn. nov.**

The genus ***Chilades*** MOORE, [1881] (figs. 1, 2)

Diagnosis – Wings: Small to large sized polyommataines (FW length between 1.5 and 3.5 cm) with hindwing tail present in many cases; male ground colour bluish, usually with antemarginal HW orange-coloured spots, females generally brown. Hindwing ventrum with extended white elements surrounding the usual polyommataine pattern. Genitalia: Male genital uncus and gnathos long and slender, aedeagus relatively large compared to other structures, suprazonal portion equal or slightly shorter in length than subzonal portion. Female genitalia with long and relatively wide, membranous, and evertable ductus bursae, terminalia sclerotized and tubular.

Distribution – Palaeotropical and Palaeartic.

Taxonomy – The following taxa previously regarded as valid genera or subgenera can be considered as synonyms; listed in alphabetic order: *Edales* SWINHOE, [1910]; *Freyeria* COURVOISIER, 1920; *Lachides* NEKRUTENKO, 1984; and *Luthrodes* H. H. DRUCE, 1895, all **syn. nov.**

The genus ***Madeleinea*** BÁLINT, 1993 (figs. 11, 12)

Diagnosis – Wings: Small or medium sized polyommataines (FW length between 1.5 and 3 cm), hindwing usually without tails; male ground colour bluish, females generally brown. Hindwing ventrum with ityloid pattern (cf. NABOKOV, 1945) comprised of a wide submedian wavy band and intercellular spaces filled with gleaming white or silvery scales. Genitalia: Male aedeagus slender with pointed suprazonal element slightly longer than subzonal element and slightly curved in lateral view. Female genitalia with evertable ductus bursae digital or quadrate-shaped in the sclerotized terminalia.

Distribution – Neotropical.

Taxonomy – The genus was very recently revised by BÁLINT & JOHNSON (1995c). The genus *Nivalis* BALLETO, 1993 was very recently synonymized under *Madeleinea* (BÁLINT, 1995b).

The genus ***Paralycaeides*** NABOKOV, 1945 (figs. 13, 14)

Diagnosis – Wings: Small polyommataines (FW length between 1.5 and 2 cm), hindwing tail sometimes present; male ground colour brown often with bronze suffusion, females generally brown. Hindwing ventrum with usual polyommataine pattern but often marked with extended or interconnected silvery suffusions. Genitalia: Male genital aedeagus stout with somewhat pointed suprazonal element shorter than subzonal element. Female genital ductus bursae evertable, strong, and with heavily sclerotized terminobasal plate.

Distribution. Neotropical.

Taxonomy – The genus *Boliviella* BALLETO, 1993 was very recently synonymized under *Paralycaeides* (BÁLINT, 1995b).

The genus ***Plebejus*** KLUK, 1802 (figs. 9, 10)

Diagnosis – Wings: Generally medium sized polyommataines (FW length between than 2 and 3 cm), male ground colour bluish, females generally brown. Hindwing ventrum with usual polyommataine pattern. Genitalia: Male genitalia with slender and long uncus and gnathos, valva often with autapomorphic structures (ampullary process or trifold furca, strongly developed apical dentation). Aedeagus with strong suprazonal element, more or less pointed, and strong subzonal element, equal or shorter in length with subzonal element. Female genital ductus bursae evertable, strong with a weakly sclerotized central tube and notable edges along terminal opening.

Distribution – Holarctic.

Taxonomy – The following taxa previously regarded as valid genera or subgenera can be considered as synonyms of *Plebejus*; listed in alphabetic sequence: *Alpherakya* ZHDANKO; *Lycaeides* HÜBNER, [1819]; *Maurus* BALINT, 1991; *Plebejides* SAUTER, 1968 and *Plebulina* NABOKOV, 1945, all **syn. nov.**

The genus ***Pseudolucia*** NABOKOV, 1945 (figs. 3, 4)

Diagnosis – Wings: Small or medium sized polyommata (FW length between 1.5 and 3 cm); hindwing without tails; male ground colour greenish or bluish often overlaid (especially on forewing) with orange suffusion; females generally brown, often overlaid with suffusive orange. Hindwing ventrum with ityloid pattern except in most primitive (*chilensis*) lineage, former often coalesced into disruptive submedian V-shaped pattern. Primitive lineage with normal polyommata markings. Genitalia: Male genital aedeagus slender and long with heavily sclerotized sagum (in *chilensis*- and *collina*-species groups) or membranous, hardly discernable sagum (in *plumbea*- and *sibylla*-species groups) with pointed suprazonal element generally shorter in length than that of the subzonal element. Female genital ductus bursae evertable with strongly sclerotized terminalia, rather variable in shape.

Distribution – Neotropical.

Taxonomy – Based on strong morphological unity, the following generic names erected by BALLETO (1993) were synonymized very recently by the senior author: *Cherchiella*, *Facula* and *Pallidula* (see BALINT, 1995b).

Note – External divergence may reflect a mimicry ring based on toxic *Cuscuta* (Cuscutaceae) feeding by the primitive (*chilensis*) lineage. In more derived congeners vivid dorsal orange suffusions resemble *chilensis* while V-shaped ventral ityloid patterns act as disruptive camouflage during perching and predator avoidance behavior (cf. BENYAMINI, 1995: fig. G and pp. 45–48).

The genus ***Polyommatus*** LATREILLE, 1804 (figs. 15, 16)

Diagnosis – Wings: Generally medium sized polyommata (FW length between 2 and 3 cm); male ground colour bluish or greenish and often with bronze suffusion, females generally brown. Hindwing ventrum with usual, but extended, polyommata pattern. Genitalia: Male genital aedeagus slender, suprazonal element conspicuously short with produced or parallel lateral edges. Female genital ductus bursae evertable and very long, with simple, sclerotized, anterior basal lamella.

Distribution – Palearctic.

Taxonomy – The following taxa previously regarded as valid genera or subgenera can be considered as synonyms of *Polyommatus*, listed in alphabetic sequence: *Bryna* EVANS, 1912; *Cyaniris* DALMAN, 1816; *Elviria* ZHDANKO, 1994; *Meleageria* DE SAGARRA, 1925; *Kretania* BEURET, 1959; *Lysandra* HEMMING, 1933; *Neolysandra* KOÇAK, 1977; *Paragrodiaetus* ROSE & SCHURIAN, 1977; *Plebicula* HIGGINS, 1969 and *Subly Sandra* KOÇAK, 1977, all **syn. nov.**

### **Species Diversity of the *Polyommatus* Section**

Only the generic and specific names are given. Specific names are listed in alphabetic order. Genera are listed according to relationships inferred from the branching diagram (fig. 22) (adjusted, as appropriate, to linear taxonomic sequence). Further historical taxonomic data (type species, place of original description, original combinations, synonyms, location of type specimens, type locality) are readily obtained from the Catalogue of BRIDGES (1994) and therefore not repeated here. Subsequent annotations are provided to certain individual species groups. A plus-sign (+) aside individual

species means that primary type specimens were studied or lectotype (and in some cases neotype) designations will be provided later in a separate work (BÁLINT, in prep.). Etymologies for new replacement names required by the ICZN Code are also included in subsequent annotations and keyed within the list by an asterisk (\*).

Lists for the neotropics reflect the work of both the present authors; those for the rest of the world are derived solely from the work of the senior author.

In the list below, a generalized distribution for each hierarchical taxonomic grouping is provided. The basis of the terminology is clarified in the previous entry Material and Methods.

Genus ***Pseudolucia*** NABOKOV, 1945 [NT: S Andes and central SA]

***andina***-group (= *Cherchiella*) [NT: S Andes and austral SA]

- andina* (BARTLETT-CALVERT, 1894) (+) – NT: high Andes of C Chile and Argentina (Mendoza).
- asafi* BENYAMINI, BÁLINT and JOHNSON, 1995 (+) – NT: high Andes of S Chile.
- avishai* BENYAMINI, BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of C Chile.
- lanin* BÁLINT and JOHNSON, 1993 (+) – NT: Patagonia (Chile and Argentina).
- magellana* BENYAMINI, BÁLINT & JOHNSON, 1995 (+) – NT: Tierra del Fuego.
- neuqueniensis* BÁLINT & JOHNSON, 1995 (+) – NT: Patagonia (Chile and Argentina).
- scintilla* (BALLETO, 1993) – NT: high Andes of C Chile.
- spec. nov. prope andina* (ex Cuesta la Dormida) – NT: Pacific coast of Chile.
- spec. nov. prope neuqueniensis* (ex Chico, Chile) – NT: Patagonia (Chile).

***chilensis***-group (= *Pseudolucia* s. str., *Pallidula*) [NT: montane SE Brasil and austral SA]

- charlotte* BÁLINT & JOHNSON, 1993 (+) – NT: Patagonia (Chile and Argentina).
- chilensis* (BLANCHARD, 1852) (+) – NT: Pacific coast of Chile and Peru (?).
- parana* BÁLINT, 1993 (+) – NT: subcoastal Cordilleras in SE Brasil.
- vera* BÁLINT & JOHNSON, 1993 (+) – NT: Patagonia (Chile and Argentina).

***collina***-group [NT: Chile]

- benyamini* BÁLINT & JOHNSON, 1995 (+) – NT: Pacific coast of C Chile.
- spec. nov. prope benyamini* (ex Cuesta la Dormida, Chile) – NT: subcoastal mountains in C Chile.
- collina* (PHILIPPI, 1859) (+) – NT: Pacific coast, subcoastal mountains and high Andes of C Chile.
- spec. nov. prope collina* (Pan de Azucar, Chile) – NT: Pacific coast of N Chile.

***lyrnessa***-group [NT: S Andes and austral SA]

- humbert* BÁLINT & JOHNSON, 1995 (+) – NT: NW Argentina (Salta).
- lyrnessa* (HEWITSON, 1874) (+) – NT: subcoastal mountains of C Chile.
- shapiro* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of C Argentina (Mendoza).
- tamara* BÁLINT & JOHNSON, 1995 (+) – NT: Patagonia (Chile and Argentina).

***plumbea***-group (= *Cherchiella*, partim) [NT: S Andes and austral SA]

- annamaria* BÁLINT & JOHNSON, 1993 (+) – NT: high Andes of C Chile.
- clarea* BÁLINT & JOHNSON, 1993 (+) – NT: high Andes of C Chile.
- grata* (KÖHLER, 1934) (+) – NT: Patagonia (Chile and Argentina).
- hazeorum* BÁLINT & JOHNSON, 1993 (+) – NT: high Andes of C Chile.
- patago* (MABILLE, 1899) (+) – NT: Patagonia (Argentina).
- plumbea* (BUTLER, 1881) (+) – NT: high Andes of C Chile.
- whitakeri* BÁLINT & JOHNSON, 1995 (+) – NT: Patagonia (Argentina).
- zina* BENYAMINI, BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of C Chile.

**sibylla**-group (= *Facula*) [NT: S Andes]

- aureliana* BÁLINT & JOHNSON, 1993 (+) – NT: high Andes of N Chile.  
*argentina* (BALLETO, 1993) (+) – NT: high Andes of C Chile and C Argentina.  
*oligocyanea* (URETA, 1956) (+) – NT: high Andes of N Chile.  
*penai* BÁLINT & JOHNSON, 1993 (+) – NT: high Andes of N Chile.  
*sibylla* (KIRBY, 1871) (+) – NT: high Andes of N Chile.  
*talia* BENYAMINI, BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of N Chile, adjacent Argentina.

Genus **Aricia** R. L., 1817 [Laurasia]

**agestis**-group (= *Aricia* s. str.)<sup>2</sup> [PA: including N Africa and Canary Islands]

- agestis* (DENIS & SCHIFFERMÜLLER, 1775) – PA: Europe, Caucasus region, Asia Minor, Levant, mountains of C Asia.  
*allous* (GEYER, [1836]) – PA: Europe (Alps).  
*artaxerxes* (FABRICIUS, 1793) – PA: Europe (N Britannia and S Scandinavia).  
*cramera* (ESCHSCHOLTZ, 1821) – PA: Canary Islands, NW Africa, SW Europe (Iberia).  
*mandschurica* (STAUDINGER, 1892) – PA: Amur region.  
*inhonora* (JACHONTOV, 1909) – PA: E Europe, Caucasus region, Siberia, mountains of S Siberia, Mongolia.  
*montensis* VERITY, 1928 – PA: Europe (Iberia).  
*issekutzi* (BALOGH, 1956) (+) – PA: SE Europe (Carpathians and Balkans), Asia Minor.  
*transalica* (OBRAZTSOV, 1935) – PA: mountains of C Asia, Himalayas.

**anteros**-group (= *Ultraaricia*) [PA: SE Europe and C Asia]

- anteros* (FREYER, 1839) (+) – PA: SE Europe (Balkans), Asia Minor, Levant.  
*bassoni* LARSEN, 1974 (+) – PA: Levant.  
*crassipuncta* (CHRISTOPH, 1893) (+) – PA: Kurdistan.  
*morroneis* (RIBBE, 1910) – PA: Europe (Iberia).  
*vandarbani* (PFEIFFER, 1937) (+) – PA: Elburs region.

**chinensis**-group (= *Umpria*) [PA: Eurasia and N China]

- chinensis* (MURRAY, 1874) (+) – PA: mountains of C Asia, mountains of S Siberia, Mongolia, N China.  
*myrmecias* (CHRISTOPH, 1877) (+) – PA: mountains of C Asia.  
*scythissa* NEKRUTENKO, 1985 – PA: Caucasus region.

**eumedon**-group<sup>3</sup> (= *Eumedonia*) [PA: Eurasia and N China]

- annulata* (ELWES, 1906) (+) – PA: E Himalayas (Tibet).  
*astorica* (TYTLER, 1925) (+) – PA: W Himalayas.  
*eumedon* (ESPER, 1780) – PA: Europe, Caucasus region, Asia Minor, Siberia, S Siberian mountains, Mongolia, Amur region.

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- 2 Taxonomy in this group, containing only discoloured taxa (see below), is best to understood by the superspecies concept (cf. VARGA, 1968). Accordingly, adopted here and expanded for the range of the entire group is the arrangement of KUDRNA (1986: 172–173), who divided the complex's European representatives into several allopatric morphospecies.
- 3 NABOKOV apparently did not examine an authentic representative of *A. persephatta*, he wrote that the taxon belonged to "Glaucopschyinae", and not the "Plebejinae" (NABOKOV, 1945: 48, footnote). From these notes, it appears NABOKOV most likely confused *persephatta* with the "look-alike" sympatric species *Praephilotes anthracias* (CHRISTOPH, 1887) or one of the numerous species of *Turanana* BETHUNE-BAKER, 1916. FORSTER considered *persephatta* congeneric with *semiargus* in the subgenus *Cyaniris* of *Polyommatus* (FORSTER, 1938: 114), noting that precise elaboration of the taxonomic make-up of *Cyaniris* posed a very difficult problem. LUKHTANOV & LUKHTANOV (1994: 291) followed FORSTER, placing

*kogistana* (GRUM-GRSHIMAILO, 1888) (+) – PA: mountains of C Asia.  
*lamasem* (OBERTHÜR, 1910) (+) – PA: E Himalayas (Tibet).  
*mylitta* HEMMING, 1932 (+) – PA: Levant (Lebanon).  
*persephatta* (ALPHERAKY, 1881) (+) – PA: mountains of C Asia.  
*privata* (STAUDINGER, 1895) – PA: W Himalayas.  
*timida* (GRUM-GRSHIMAILO, 1885) (+) – PA: mountains of C Asia.

**icarioides**-group (= *Icaricia*)<sup>4</sup> [NA: North America]

*acmon* (WESTWOOD, [1852]) – NA: western NA from S Canada, W montane Mexico, vagrant in northeastward US in Sonoran/Canadian life zones.  
*icarioides* (BOISDUVAL, 1852) (+) – NA: western United States, extreme SW Canada.  
*lupini* (BOISDUVAL, 1869) (+) – NA: western US in Sierra Nevada and coastal ranges, eastward in Nevada ranges.  
*neurona* (SKINNER, 1902) – NA: montane S California.  
*saepiolus* (BOISDUVAL, 1852) (+) – NA: east Alaska, Rocky Mountains, Great Lakes region east to Atlantic coast.  
*shasta* (EDWARDS, 1862) – NA: western Great Plains, C Rocky Mountains, Great Basin, Sierra Nevada.

**nicias**-group (= *Pseudoaricia*) [PA: Europe, C Asia and N China]

*dorsumstellae* (GRAVES, 1923) (+) – PA: Elburs regions.  
*hyacinthus* (HERRICH-SCHÄFFER, [1847]) (+) – PA: Europe (extinct), Asia Minor, Levant.  
*isaurica* (STAUDINGER, 1871) – PA: Kurdistan, Levant.  
*nicias* (MEIGEN, 1829) – PA: Europe (Alps, Balkans, Scandinavia), mountains of S Siberia, N Mongolia.

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*persephatta* after *semiargus*. Examination of the problem in the present study indicates the male genital aedeagus (with a pointed suprazonal element) and the female terminalia (with a central sclerotized tube) do, in fact, support the placement of *persephatta* in this species group. Also, as a result of research in the present investigation based on study of type materials (BMNH, *P. annulatus*, holotype examined; ZSM, *P. tibetanus*, holotype examined) "*Polyommatus annulata*" ELWES, 1906 proves identical with "*Polyommatus (Lycaeides) tibetanus*" FORSTER, 1940 (**syn. nov.**). In addition, *P. lamasem*, often misplaced in *Agriaedes* (e. g. D'ABRERA, 1993: 493), obviously belongs to the *eumedon* species group based on its morphology.

- 4 According to NABOKOV (1944: 104) the taxon *saepiolus* belonged to *Plebejus* s. str. (e. g. *argus* group of *Plebejus* cf. HOWE, 1975). However, the male genital aedeagus (with a pointed and elongate suprazonal element) and the female terminalia (with a sclerotized habitus) obviously indicate NABOKOV'S view was incorrect. Considering the genital features, especially the slender aedeagus with large and pointed suprazonal element, the taxon belongs to the Nearctic stock of *Aricia*. Such genital features characterize all the polyommata in North America, except *Plebejus idas* and its relatives, and *Albulina optilete*. Our treatment of the *icarioides*-group herein follows well-established precedent for the Nearctic fauna, it having been the subject of considerable biological and field research by North American workers over the years. Species concepts preferred by North American common usage follow the "Rassenkreis" concept (see DOWNEY, 1962; DOWNEY et al. 1961, 1964) and all the published general synonymic lists and manuals. This must be explained briefly because it results in the Nearctic and Palaearctic concepts herein being somewhat imbalanced. For the Old World the Rassenkreis concept was omitted by us in the case of the *pylaon*-group and *idas*-group, since within the Rassenkreis concept, FORSTER (1936, 1938) noted the major "races" could be morphologically identified. The same is true in the Nearctic; however, Nearctic taxonomists react with extreme negativity to any upset of long term stability, perhaps with good reason (see EHRlich & MURPHY, 1973). We point out, therefore, that from a morphological perspective the taxa *monticola* CLÉMENTE and *chlorina* SKINNER are distinctive but are here considered subspecies of *lupini*; similarly, the taxon *pheres* BOISDUVAL (+) is distinctive in morphology but here considered a subspecies of *icarioides*. Had we listed these taxa according to a larger super-species concept, with each as morphospecies, we doubt whether North American taxonomists would have understood our motivation and, instead, supposed we were ignorant of the biological data supporting the Rassenkreis in common usage.

*teberdina* (SHELJUZKO, 1934) – PA: Caucasus region.  
*torulensis* HESSELBARTH & SIEPE, 1993 – PA: Kurdistan.

Genus **Madeleinea** BÁLINT, 1993 [NT: high Andes]

**huascarana**-group [NT: high C Andes]

*colca* BÁLINT & LAMAS, 1996 (+) – NT: high Andes of C and S Peru.  
*huascarana* BÁLINT & LAMAS, 1994 (+) – NT: high Andes of N Peru.  
*lea* BENYAMINI, BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of S Peru and Bolivia.

**lolita**-group [NT: high C Andes]

*lolita* BÁLINT, 1993 (+) – NT: high Andes of N Peru.

**pacis**-group [NT: Andes and austral SA]

*cobaltana* BÁLINT & LAMAS, 1994 (+) – NT: high Andes of C and S Peru.  
*gradoslamsi* spec. nov. (+) – NT: high Andes of C Peru.  
*ludicra* (WEYMER, 1890) (+) – NT: high Andes of S Peru and NE Chile.  
*moza* (STAUDINGER, 1892) (+) – NT: high Andes of Bolivia, Argentina and Patagonia (only in Argentina), Paraguay (?).  
*pacis* (DRAUDT, 1921) (+) – NT: high Andes of SE Peru.  
*pelorias* (WEYMER, 1890) (+) – NT: high Andes of S Peru and NE Chile.  
*sigal* BENYAMINI, BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of S Peru and NE Chile.

**koa**-group [NT: Andes]

*bella* BÁLINT & LAMAS, 1995 (+) – NT: high Andes of C Peru.  
*carolityla* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of Ecuador.  
*koa* (DRUCE, 1896) (+) – NT: high Andes of C and S Ecuador and N Peru.  
*nodo* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of S Colombia.  
*odon* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of Ecuador.  
*tintarrona* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of C and S Peru.  
*vokoban* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of Ecuador.

Genus **Chilades** MOORE, [1881] [OR, AFR: Old World Gondwana – India, Africa, SW Pacific; and, SW Palaeartic]

**cleotas**-group (= *Luthrodes*, *Edales*) [OR: India and SW Pacific]

*boopsis* (FRUHSTORFER, 1897) (+) – OR: Sulawesi.  
*buruana* (HOLLAND, 1900) – OR: Buru.  
*cleotas* (GUÉRIN-MÉNEVILLE, [1831] – OR: New Guinea.  
*mindora* (FELDER & FELDER, 1865) (+) – OR: Philippines.  
*pandava* (HORSFIELD, [1829]) – OR: Java, Sumatra.  
*peripatria* HSU, 1989 – OR: Taiwan.

**galba**-group (= *Lachides*)<sup>5</sup> [PA: SW Palaeartic]

*galba* (LEDERER, 1855) – PA: Asia Minor, Levant, deserts of C Asia.  
*contracta* (BUTLER, 1880) (+) – PA: southern C Asia.  
*ella* (BUTLER, 1881) (+) – PA: southern C Asia.

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5 According to the examined primary type material of *Catochrysops ella*, the taxon seems to be a good species, belonging to this genus. It was very recently collected in a short series by H. HACKER (Germany, Staffelfstein) in India (Rajasthan, 20 km W Jodhpur).

***lajus***-group (= *Chilades*, *Freyeria*)<sup>6</sup> [AFR: Africa, extreme S Palaearctic]  
*alberty* (BUTLER, 1901) (+) – AFR: Uganda.  
*eleusis* (DEMAISON, 1888) (+) – AFR: Arabia and Sudan.  
*elicola* (STRAND, 1911) (+) – AFR: Ethiopia and S Arabia.  
*kedonga* (GROSE-SMITH, 1898) (+) – AFR: E equatorial Uganda, S Kenya and Ethiopia.  
*lajus* (STOLL, [1780]) – AFR: southern C Asia.  
*nigeriae* (E. SHARPE, 1902) – AFR: equatorial W Africa.  
*parrhasius* (FABRICIUS, 1793) – AFR: E Arabia; OR: S India and Sri Lanka.  
*putli* (KOLLAR, [1844]) (+) – PA: N India.  
*sanctithomae* (SHARPE, 1893) (+) – AFR: S Africa.  
*serrula* (MABILLE, 1890) (+) – AFR: C Africa.  
*minuscula* (AURIVILLIUS, 1909) – AFR: Madagascar.  
*trochylus* (FREYER, 1844) (+) – PA: SE Europe (Balkans), Asia Minor, Levant, C Asia; AFR: everywhere.

Genus ***Plebejus*** KLUK, 1802 [PA, NA: Laurasia]

***ardis***-group<sup>7</sup> [PA: C Asia and W Himalayas]  
*ardis* BÁLINT & JOHNSON, nom. nov. (\*) – PA: mountains of C Asia.  
*badachshana* (FORSTER, 1972) (+) – PA: mountains of C Asia.  
*baroghila* (TYTLER, 1926) (+) – PA: W Himalayas.  
*firuskuhi* (FORSTER, 1940) (+) – PA: W Himalayas.  
*kwaja* (EVANS, 1932) (+) – PA: mountains of C Asia.

***argus***-group (= *Plebejus* s. str.)<sup>8</sup> [PA: Eurasia including Japan]  
*aegidon* (GERHARD, 1853) – PA: mountains of C Asia.  
*argus* (LINNAEUS, 1758) – PA: Europe, Caucasus region, W Siberia.  
*bella* (HERRICH-SCHÄFFER, [1844]) (+) – PA: Asia Minor, Kurdistan, Levant.  
*corsicus* (BELLIER, 1862) (+) – PA: Europe (Corsica, Sardinia).  
*hipochyonus* (RAMBUR, 1858) – PA: Europe (Iberia).  
*micrargus* (BUTLER, 1878) (+) – PA: Japan.

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6 The Afrotropical representatives of the genus are little known, we primarily follow the recent catalogue of ACKERY et al. (1995).

7 Replacement name for *Lycaena eversmanni* STAUDINGER, 1894, is needed because it is a homonym of *Lycaena eversmanni* LANG, 1884. Therefore we employ a "NABOKOVIAN name" suggested to us by the International VLADIMIR NABOKOV Society (see Acknowledgements). The new name is *Plebejus ardis* BÁLINT & JOHNSON, **nom. nov.** Its etymology is as follows, provided us by Dr. ELLENDEA PROFFER, a current MACARTHUR Fellow who, with her late husband CARL, produced some of the first scholarly monographs concerning NABOKOV's literary work. Dr. PROFFER notes that "Ardis" was the name of the great estate ("Ardis Hall") in NABOKOV's novel *Ada*, where Van and Ada (NABOKOV's only lepidopterist heroine) began their life-long love affair. "Ardis" was also subsequently employed in the name of a publishing house (Ardis Publishers) dedicated to promoting Russian literature in English. A "NABOKOVIAN" replacement name is appropriate here since NABOKOV (NABOKOV, 1949:485, pl. 1, fig. 41 and pl. 8, fig. 28) originally opined concerning the status of this taxon.

8 The spelling "*Plebejus*" is based on MELVILLE & SMITH (1987: 151) (cf. NEKRUTENKO, 1985: 83 and 128, footnotes). *Plebejus argus* s.l. is a morphological complex (FORSTER 1936) which suggests further diversity in its ecological context (RODRIGUEZ et al., 1991; THOMAS, 1985 and personal observations of the senior author in the Carpathian Basin and Dobrogea, Roumania). There are apparently numerous taxa with distinct morphologies and, accordingly, the group requires detailed taxonomic revision. Tentatively, we divide the group into several morphospecies according to FORSTER's subspecific division.

**idas**-group (= *Lycaeides*, *Plebulina*)<sup>9</sup> [PA, NA: Holarctic]  
*agnata* (STAUDINGER, 1889) – PA: mountains of C Asia.  
*anna* (EDWARDS, 1861) – NA: eastern N. America.  
*argyrognomon* (BERGSTRÄSSER, 1779) – PA: Europe, Caucasus region, Siberia, mountains of S Siberia, Mongolia, Amur region.  
*baldur* (HEMMING, 1934) (+) – PA: Kurdistan, Levant (Lebanon).  
*belleri* (OBERTHÜR, 1910) (+) – PA: Europe (Corsica).  
*christophi* (STAUDINGER, 1874) – PA: Caucasus region, Kurdistan, deserts in C Asia.  
*emigdionis* (GRINNEL, 1905) – NA: California.  
*ida* (GRUM-GRSHIMAILO, 1891) (+) – PA: mountains of S Mongolia, E Himalayas (Tibet).  
*idas* (LINNAEUS, 1758) – HA: Europe, Siberia, mountains of S Siberia, Yakutia, Alaska.  
*iburiensis* (BUTLER, [1882]) (+) – PA: Japan.  
*melissa* (EDWARDS, 1872) – NA: western N America to C Mexico.  
*naruenta* (COURVOISIER, 1913) (+) – PA: mountains of C Asia and S Siberia, W Mongolia.  
*nevadensis* (OBERTHÜR, 1896) (+) – PA: Europe (Iberia).  
*planorum* (ALPHÉRAKY, 1881) – PA: deserts of C. Asia, S Mongolia, N China.  
*samudra* (MOORE, [1875]) (+) – PA: W Himalayas.  
*subsolanus* (EVERSMANN, 1851) – PA: mountains of S Siberia, N Mongolia, Amur region.  
*tancredi* (GRAESER, 1888) – PA: Siberia, Yakutia. (? NA: Alaska).

**lucifera**-group<sup>10</sup> [PA: Himalayas and C and NE Asia]  
*lucifera* (STAUDINGER, 1867) – PA: Siberia, mountains of S Siberia, Mongolia.  
*lucifuga* (FRUHSTORFER, 1915) (+) – PA: E Himalayas (Tibet).  
*themis* (GRUM-GRSHIMAILO, 1891) (+) – PA: mountains of C Asia.

**pylaon**-group<sup>11</sup> (= *Plebejides*, *Maurus*) [Eurasia and N Africa]  
*allardi* (OBERTHÜR, 1874) (+) – PA: NW Africa (SE Morocco, Algeria, Lybia).  
*beani* BÁLINT & JOHNSON, nom. nov. (\*) – PA: mountains of C Asia, Himalayas.

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- 9 The widely distributed *idas* group has several isolated taxa in the southern Palaearctic region. They are tentatively considered here as distinct morphospecies following FORSTER's (1936) subspecific division. A geographically isolated taxon of the group, *corsicus*, has already been classified as an allopatric morphospecies by KUDRNA (1986: 173). *Plebejus naruenta* (COURVOISIER, 1913) is sympatric and partly synchronic with *P. subsolanus*, *P. idas* and *P. argyrognomon* in NW Mongolia (BÁLINT: Lycaenids of Mongolia, in prep.). Superficially it is easy to determine, because it is larger than the Mongolian *idas* having a more rounded forewing and the hindwing marginal area has a row of large gleaming spots. FORSTER also discussed the taxon before the taxon *ismenias* as ssp. *tshimgana* (FORSTER, 1936:103–104). The type of *Lycaena idas tshimgana* FORSTER, 1936 was examined (holotype ZSM). The taxon proved identical with the mentioned *P. naruenta*. Therefore *Lycaena idas tshimgana* FORSTER, 1936 (**syn. nov.**) = *Lycaena argus* f. *naruenta* COURVOISIER, 1913. The entire group obviously needs taxonomic revision, especially considering that, in the Nearctic region, not only do *idas* and *melissa* occur but also a third taxon, tentatively listed here as *anna*. The Nearctic taxon *idas* should be identical with *scudderii* of NABOKOV (1943). According to superficial wing pattern and genital structures the apparently relict Californian polyommata taxon *emigdionis* belongs to this group. It must be mentioned that *P. emigdionis* has a peculiar life history recorded by BALLMER & PRATT (1988) suggesting a more complex relationship with ants (cf. JUTZELER, 1989, for *idas*) as FIEDLER (1991) suggested for the group.
- 10 *P. themis* and *P. lucifuga* are sympatric in Tibet (specimens at BMNH). The smaller *P. lucifera* is a widely distributed taxon in southern Siberia and Mongolia. In addition, research for the present study indicates that *Vacciniina lornex* HIGGINS, 1981 (type locality: Novokuznek, Siberia; holotype examined at BMNH) is a subjective synonym of *P. lucifera selengensis* FORSTER, 1940 (**syn. nov.** [the synonymy listed by BRIDGES, 1994 is based on the present publication manuscript and was provided to him by the senior author in litt.; it is formalized here]). The biology of this Central Asian species group, as well as the biology of the possibly most closely related *ardis*-group, is unknown.
- 11 The taxa *sephirus-nichollae-zephyrinus-usbekus* form a "superspecies complex"; but all of them can be separated by their wing pattern (cf. BEURET, 1961: 341) and according to the shape of the male genital ampullary process situated on the inner side of the valvae. The taxon *pylaon* is sympatric with

*hespericus* (RAMBUR, 1839) (+) – PA: Europe (Iberia).  
*martini* (ALLARD, 1867) (+) – PA: NW Africa (Morocco, Algeria).  
*nichollae* (ELWES, 1901) (+) – PA: Levant.  
*patriarcha* BÁLINT, 1992 (+) – PA: mountains of C Asia.  
*philbyi* GRAVES, 1925 (+) – PA: deserts of Levant.  
*pylaon* (FISCHER VON WALDHEIM, 1832) (+) – PA: Europe (Volga and Dnepr region), Siberia, mountains of S Siberia, N Mongolia.  
*sephirus* (FRIVALDSZKY, 1835) (+) – PA: E Europe, Caucasus region, Asia Minor.  
*trappi* VERITY, 1927 (+) – PA: Europe (Alps).  
*usbekus* (FORSTER, 1939) (+) – PA: mountains of C Asia.  
*vogelii* (OBERTHÜR, 1910) (+) – PA: NW Africa (high Atlas in Morocco).  
*zephyrinus* (CHRISTOPH, 1884) (+) – PA: mountains of C Asia.

**sarta**-group (= *Alpherakya*)<sup>12</sup> (\*) [PA: C Asia and W Himalayas]

*bellona* (GRUM-GRSHIMAILO, 1888) (+) – PA: mountains of C Asia.  
*devanicus* (MOORE, 1874) (+) – PA: W Himalayas.  
*pilgram* BÁLINT & JOHNSON, nom. nov. (\*) – PA: mountains of C Asia.  
*sarta* (ALPHERAKY, 1881) (+) – PA: mountains of C Asia.

Genus **Paralycaeides** NABOKOV, 1945 [NT: Andes and austral SA]

**shade**-group [NT: high C Andes]

*shade* BÁLINT, 1993 (+) – NT: high Andes of C Peru.

**vapa**-group (= *Boliviella*) [NT: Andes and austral SA]

*hazelea* BÁLINT & JOHNSON, 1995 (+) – NT: high Andes of S Peru.  
*inconspicua* (DRAUDT, 1921) (+) – NT: high Andes of C and S Peru.  
*vapa* (STAUDINGER, 1894) (+) – NT: high Andes of S Peru, Bolivia, NE Chile, Argentina (also in N Patagonia).

Genus **Agriades** HÜBNER, [1819] [PA, NA: Eurasia and Beringia]

**aquilo**-group (= *Agriades* s. str.) [PA, NA: montane Eurasia and western NA]

*aquilo* (BOISDUVAL, 1832) (+) – PA: Europe (Scandinavia), Siberia, Yakutia.

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*zephyrinus* in the Altai region and with *sephirus* in the Volga region (cf. LUKHTANOV & LUKHTANOV, 1994: figs. 328, 329). *Plebejus beani* BÁLINT & JOHNSON, nom. nov. is a replacement name for *Lycaena indica* EVANS, 1925, which is a homonym of *Lycaena indica* MURRAY, 1874. The name is dedicated to Rev. ALAN BEAN (Oxford, UK), who widely published important papers on the life history of certain Indian lycaenids. Research for the present study indicates that *Plebejus balinti* D'ABRERA, 1993 (type locality: Tura) is a subjective synonym (**syn. nov.**) of *Cupido buddhista* (ALPHERAKY, 1881). The male genitalia shows typical *Cupido* structures.

- 12 *Lycaena serica* GRUM-GRSHIMAILO, 1902, is a homonym of *Lycaena serica* C. FELDER, 1862, and a replacement name is required. We employ a "NABOKOVIAN name" suggested to us by the International VLADIMIR NABOKOV Society (see Acknowledgements). The new name is *Plebejus pilgram* BÁLINT & JOHNSON, nom. nov. Its etymology is as follows, provided us by Dr. SIMON KARLINSKY, recently retired Professor of Russian Literature at the University of California (Berkeley), a pioneer in NABOKOV studies: "Pilgram" was the protagonist in NABOKOV's story "The Aurelian". The German owner of a butterfly shop, he dreamed all his life of hunting butterflies in exotic locales but, as he was about to realize his dreams, died of a heart attack. This "NABOKOVIAN" replacement name is appropriate here since, like Pilgram, NABOKOV moved from long-nurtured interest in the Palaearctic fauna to a fascination with New World blues. The result was his seminal work on the taxonomy of Neotropical polyommatae (NABOKOV, 1945).

*franklinii* (CURTIS, 1835) – NA: Alaska.

*glandon* (PRUNNER, 1798) – PA: Europe (Alps).

*rusticus* (EDWARDS, 1865) (+) – NA: California

*wosnesenskyi* (MÉNÉTRIÉS, 1857) – PA: mountains of S Siberia, Mongolia and Amur region.

**ellisi**-group<sup>13</sup> [PA: Himalayas]

*ellisi* (MARSHALL, 1882) (+) – PA: C Himalayas.

*errans* (RILEY, 1927) (+) – PA: C Himalayas.

*janigena* (RILEY, 1932) (+) – PA: C Himalayas.

*jaloka* (MOORE, [1875]) (+) – PA: Himalayas.

*kurtjohnsoni* BÁLINT, spec. nov. – PA: C Himalayas.

*morsheadi* (EVANS, 1922) (+) – PA: E Himalayas (Tibet).

**pyrenaicus**-group [PA: Europe and C Asia]

*aegargus* (CHRISTOPH, 1873) (+) – PA: mountains of C Asia.

*dardanus* (FREYER), 1844 (+) – PA: Europe (Balkans?), Asia Minor.

*ergane* HIGGINS, 1981 (+) – PA: Europe (Dnepr plain).

*forsteri* SAKAI, 1972 – PA: mountains of C Asia.

*latedisjunctus* (ALBERTI, 1973) – PA: Caucasus region.

*pheretiades* (EVERSMANN, 1843) – PA: mountains of C Asia.

*pyrenaicus* (BOISDUVAL, 1840) (+) – PA: Europe (Iberia).

*zuellichi* HEMMING, 1933 (+) – PA: Europe (Iberia).

**sikkima**-group<sup>14</sup> [PA: C Asia and Himalayas]

*dis* (GRUM-GRSHIMAILO, 1891) (+) – PA: mountains of C Asia.

*luanus* (EVANS, 1925) (+) – PA: C Himalayas.

*sikkima* (BATH, 1900) (+) – PA: C Himalayas.

Genus **Albulina** TUTT, 1909 [PA, NA: Eurasia and Beringia]

**felicitis**-group (= *Patricius*) [PA: Himalayas]

*gaborronkayi* BÁLINT, spec. nov. – PA: E Himalayas (Nepal, Tibet).

*felicitis* (OBERTHÜR, 1886) (+) – PA: E Himalayas (Tibet).

*youngusbandi* (ELWES, 1906) (+) – PA: E Himalayas (Tibet).

**galathea**-group (= *Pamiria*) [PA: W and C Asia, Himalayas and N China]

*selma* (KOÇAK, 1996) (+) – PA: W Himalayas.

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13 The group is restricted to the highest ranges of the Western Himalayas and to the high plateau of Tibet and shows interesting phenotypical similarity to the Neotropical sister genus *Paralycaeides* (cf. BÁLINT & JOHNSON, 1994). Along with the light appearance of the FW discal spot (which appears to be a general polyommata response to cooler climate, cf. *Aricia artaxerxes*, *Agriades sikkima*, *A. luana*, etc.) the lunulation and pupation of the HW markings are quite analogous to that of the *vapa* group of *Paralycaeides*. D'ABRERA (1993: 493–494) figured all the taxa belonging to this species group but in the butterfly collection of the Natural History Museum, London (BMNH), where D'ABRERA's folio plates were prepared, the senior author found a further, still undescribed, taxon belonging to this group, which will be described in the Appendix.

14 This group contains an assemblage of little known taxa sharing narrowly shaped forewings with very pointed apices and short costal lengths. Their distributions are restricted to high mountain ranges of the central Himalayas and the Tibetan plateau. D'ABRERA (1993, l.c.) figured the discoloured taxa of the genus group, but he neglected to mention the taxon *Lycaena sikkima* BATH, 1900, which was also overlooked by the various volumes of SEITZ's "Die Gross-Schmetterlinge der Erde" (SEITZ, 1907–1921 and 1912–1927).

*chrysopsis* (GRUM-GRSHIMAILO, 1888) (+) – PA: mountains of C Asia.  
*galathea* (BLANCHARD, 1884) (+) – PA: W Himalayas.  
*issa* ZHDANKO, 1994 – PA: mountains of C Asia.  
*metallica* (FELDER & FELDER, 1865) (+) – PA: Himalayas.  
*omphisa* (MOORE, [1875]) (+) – PA: Himalayas, N China.

**loewi**-group (= *Plebejidea*)<sup>15</sup> [PA: C Asia and W Himalayas]  
*chamanica* (MOORE, 1884) (+) – PA: deserts of Levant.  
*fergana* (STAUDINGER, 1881) – PA: mountains of C Asia.  
*loewi* (ZELLER, 1847) – PA: Asia Minor, Levant, Kurdistan, Elbrus region, mountains of C Asia.  
*rosei* (ECKWEILER, 1989) – PA: Kurdistan.  
*sanoga* (EVANS, 1925) (+) – PA: W Himalayas.

**morgianus**-group (= *Farsia*) [PA: C Asia and W Himalayas]  
*hanna* (EVANS, 1932) (+) – PA: W Himalayas.  
*iris* (STAUDINGER, 1886) – PA: mountains of C Asia.  
*morgianus* (KIRBY, 1871) (+) – PA: mountains of C Asia.  
*omotoi* (FORSTER, 1972) (+) – PA: mountains of C Asia.  
*rutilans* (STAUDINGER, 1886) – PA: mountains of C Asia.  
*sieversii* (CHRISTOPH, 1873) (+) – PA: mountains of C Asia.

**optilete**-group (= *Vacciniina*)<sup>16</sup> [PA, NA: Eurasia including Japan; and, Beringia]  
*alcedo* (CHRISTOPH, 1877) (+) – PA: Asia Minor, Levant, mountains of C Asia.  
*cyparissus* (HÜBNER, [1813]) – PA: Europe (Alps).  
*daisetsuzanus* (MATSUMURA, 1927) – PA: Korea, Japan.  
*optilete* (KNOCH, 1781) – HA: N and C Europe, Siberia, N Mongolia, Yakutia, Alaska.

**orbitulus**-group (= *Albulina*)<sup>17</sup> [PA: montane Eurasia]  
*amphirroae* OBERTHÜR, 1910 (+) – PA: E Himalayas (Tibet).  
*arcaseia* (FRUHSTORFER, 1916) (+) – PA: Himalayas.  
*asiatica* (ELWES, 1882) (+) – PA: mountains of C Asia, Himalayas.  
*lehana* (MOORE, 1878) (+) – PA: C Himalayas.  
*orbitulus* (DE PRUNNER, 1798) (+) – PA: Europe (Alps).  
*sajana* (HEYNE, 1895) (+) – PA: Europe (Scandinavia), Siberia, N Mongolia.  
*tibetana* D'ABRERA, 1993 (+) – PA: E Himalayas (Tibet).  
*tatsienluica* (OBERTHÜR, 1910) (+) – PA: E Himalayas (Tibet).

Genus **Polyommatus** LATREILLE, 1804 [PA: W Eurasia including N Africa]

**actinides**-group<sup>18</sup> (= *Agrodiaetus* s. l.) [PA: Eurasia including N Africa]  
*actinides* (STAUDINGER, 1886) – PA: mountains of C Asia.  
*praeactinides* (FORSTER, 1960) (+) – PA: mountains of C Asia.

15 The classification presented here is tentative. The taxon *loewi* s. l. represents several morphospecies, as already noted by BALLETO & KUĐRNA (1989: 249).

16 Besides *Plebejus idas*, *Albulina optilete* is the only polyommatine lycaenid which has a Holarctic distribution.

17 The taxon *orbitulus* is a species endemic to the western Palaearctic while its larger sister taxon, *sajana*, is widely distributed in the southern Siberian mountains and Mongolia. The sympatric taxa *asiaticus* and *lehanus* are widely distributed in the Himalayas (BÁLINT, in preparation).

18 The division of *Agrodiaetus* s. l. species groups, all of them pending revision, are primarily based on the very recent work of HESSELBARTH et al. (1994: 703–706, Table 20); LUKHTANOV (1989), CARBONELL (1993), KOÇAK (1996) and KOLEV & DE PRINS (1995) were also consulted. The *admetus* species group

*thersites* (CANTENER, 1834) – PA: NW Africa, Europe, Caucasus Region, Asia Minor, Levant, mountains of C Asia, mountains of S Siberia.

**actis**-group (= *Agrodiaetus* s. l.) [PA: Eurasia including N Africa]

- actis* (HERRICH-SCHÄFFER, 1851) – PA: Asia Minor.
- altivagans* (FORSTER, 1956) (+) – PA: Asia Minor.
- charmeuxi* (PAGÉS, 1994) – PA: Asia Minor.
- ectabanensis* (DE LESSE, 1963) (+) – PA: Asia Minor.
- firdussii* (FORSTER, 1956) (+) – PA: Kurdistan.
- gorbunovi* DANTSCHENKO & LUKHTANOV, 1994 – PA: Caucasus region.
- pfeifferi* (BRANDT, 1938) (+) – PA: Elburs region.
- turcicus* (KOÇAK, 1979) – PA: Kurdistan.
- wagneri* (FORSTER, 1956) (+) – PA: Kurdistan.

**admetus**-group (= *Agrodiaetus* s. l.) [PA: Europe and C Asia]

- admetus* (ESPER, 1758) – PA: SE Europe (Balkans).
- afghanica* (FORSTER, 1973) (+) – PA: mountains of C Asia.
- alcestis* (ZERNY, 1932) – PA: Asia Minor, Levant.
- aroeniensis* (BROWN, 1976) – PA: SE Europe (Balkans).
- budaskini* KOLEV & DE PRINS, 1995 – PA: E Europe (Crimea).
- demavendi* (PFEIFFER, 1938) (+) – PA: Caucasus region, Kurdistan, Levant.
- exuberans* (VERITY, 1926) – PA: C Europe (extinct).
- fabressei* (OBERTHÜR, 1910) (+) – PA: Europe (Iberia).
- galloi* (BALLETO & TOSO, 1979) – PA: Europe (Italia).
- humedasmae* (TOSO & BALLETO, 1976) – PA: Europe (Italia).
- interjectus* (DE LESSE, 1960) (+) – PA: Asia Minor, Kurdistan.
- mithridates* (STAUDINGER, 1879) – PA: Kurdistan, Elburs region.
- nephoiptamenos* (BROWN & COUTSIS, 1978) – PA: SE Europe (Balkans).
- paralcestis* (FORSTER, 1960) (+) – PA: SE Europe (Balkans), Asia Minor.
- ripartii* (FREYER, 1830) – PA: Europe (Iberia).
- valiabadi* (ROSE & SCHURIAN, 1977) – PA: Kurdistan.
- violetae* (GOMEZ-BUSTILLO et al., 1979) – PA: Europe (Iberia).

**carmon**-group (= *Agrodiaetus* s. l.) [PA: Asia Minor and Kurdistan]

- carmon* (HERRICH-SCHÄFFER, 1851) – PA: Asia Minor.
- cyaneus* (STAUDINGER, 1899) – PA: Asia Minor.
- diziniensis* (SCHURIAN, 1982) – PA: Kurdistan.
- kendevani* (FORSTER, 1956) (+) – PA: Kurdistan.
- merhaba* DE PRINS et. al. 1991 – PA: Kurdistan.
- pseudoxerxes* (FORSTER, 1956) – PA: Asia Minor.
- turcicus* (KOÇAK, 1977) – PA: Asia Minor.
- yurinekrutenko* (KOÇAK, 1996) – PA: Caucasus region, Kurdistan.

**coelestina**-group (= *Neolysandra*) [PA: Asia Minor, Kurdistan, Levant]

- alticola* (CHRISTOPH, 1893) (+) – PA: Caucasus region, Asia Minor, Kurdistan.
- coelestina* (EVERSMANN, 1843) – PA: Asia Minor.
- corona* (VERITY, 1936) – PA: Levant (Lebanon).

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sensu HESSELBARTH et al. is certainly polyphyletic, containing discoloured taxa of several species groups, but no specific effort has been made to assess these species groups. Note added in proof: Very recently an important compilation on *Agrodiaetus* s. l. was published as "Contributions to the systematics and biology of the *Polyommatus* (*Agrodiaetus*) species-group (Lepidoptera: Lycaenidae)", edited by W. ECKWEILER and Ch. L. HÄUSER, Nachr. ent. Ver. Apollo, Suppl. **16**, 166pp.

*diana* (MILLER, 1912) (+) – PA: Kurdistan.  
*ellisoni* (PFEIFFER, 1931) (+) – PA: Kurdistan, Elburs region.  
*fatima* (ECKWEILER & SCHURIAN, 1980) (+) – PA: Kurdistan.  
*ponticus* (COURVOISIER, 1911) (+) – PA: Asia Minor, Caucasus region.

**coridon**-group (= *Lysandra*)<sup>19</sup> [PA: Eurasia, including N. Africa, to C Asia]

*albicans* (GERHARD, 1851) – PA: Europe (Iberia).  
*apennina* (ZELLER, 1847) – PA: Europe (Italia).  
*bellargus* (ROTTEMBERG, 1775) – PA: Europe.  
*caelestissimus* (VERITY, 1921) – PA: Europe (Iberia)  
*ciscaucasicus* (JACHONTOV, 1914) – PA: Caucasus region.  
*coridon* (PODA, 1761) – PA: Europe.  
*corydonius* (HERRICH-SCHÄFFER, [1852]) – PA: Asia Minor.  
*dezinus* (DE FREINA & WITT, 1983) – PA: Kurdistan.  
*hispanus* (HERRICH-SCHÄFFER, [1852]) – PA: SW Europe.  
*nufrellensis* (SCHURIAN, 1977) (+) – PA: Europe (Corsica).  
*ossmar* (GERHARD, 1851) – PA: Asia Minor.  
*polonus* ZELLER, 1844 – PA: Europe (extinct).  
*punctiferus* (OBERTHÜR, 1876) (+) – PA: NW Africa.  
*syriacus* (TUTT, 1914) – Kurdistan, Levant.

**cornelia**-group (= *Sublysandra*)<sup>20</sup> [PA: Asia Minor, C Asia and W Himalayas]

*bilucha* (MOORE, 1884) (+) – PA: W Himalayas.  
*cornelia* (GERHARD, 1851) – PA: Asia Minor, Elburs region, mountains of C Asia.  
*isauricoides* (GRAVES, 1923) (+) – PA: Levant.  
*muetingi* (BALINT, 1992) (+) – PA: mountains of C Asia.  
*nuksani* (FORSTER, 1937) (+) – PA: mountains of C Asia.

**cyane**-group (= *Elvira*, *Rimisia*) [PA: Eurasia]

*cyane* (EVERSMANN, 1837) – PA: Europe (Volga region), Siberia, mountains of S Siberia, N Mongolia.  
*deserticolus* (ELWES, 1899) (+) – PA: mountains of C Asia, SW and C Mongolia.  
*elvira* (EVERSMANN, 1854) – PA: mountains of C Asia.  
*miris* (STAUDINGER, 1881) – PA: mountains of C Asia.

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19 Division of this group basically follows the recent revision by SCHURIAN (1989) with four exceptions based on our larger analysis of the section: 1) the peripheral and geographically isolated taxa *apennina*, *caelestissimus* and *nufrellensis* are not considered subspecies but, rather, full sister species of European *coridon*; 2) the large, dark coloured taxon *ciscaucasicus* (of which SCHURIAN saw no material; our material examined, deposited in HNHM, five males: "Russia, Caucasus region, Kislovodsk, 1990.VII.11., leg. V. LUKHTANOV"), is considered a full sister species of the smaller, lighter coloured Anatolian-Caucasian taxon *corydonius* and 3) the controversial taxon *P. polonus*, generally considered as *coridon* x *bellargus* natural hybrid in the literature, is listed as most likely an extinct species of the genus group, for the following reasons: 1. SCHURIAN crossed *bellargus* and *coridon* without positive results, 2. the taxon *polonus* fits well into the *dezinus-ossmar-corydonius* lineage of the genus group, 3. all the papers of DE LESSE concerning *P. polonus* which are mentioned in the literature cited by SCHURIAN (1989) discuss natural hybrids of *daphnis* and *coridon* (or very closely related European taxa).

20 FIEDLER & SCHURIAN (1994: 330) suggested that *cornelia* (= *candalus* HERRICH-SCHÄFFER, [1852]) is conspecific with the taxa *anatolica* KOÇAK, 1975, *isauricoides* GRAVES, 1923 and *subtilis* PAGÈS & CHARMEUX, 1992. Their results are partly reflected in the specific list but we kept *isauricoides* as a distinct species because of its isolated geographic position and peculiar wing patterns.

**dama**-group (= *Agrodiaetus* s.str.) [PA: Eurasia]

- dama* (STAUDINGER, 1892) – PA: Kurdistan, Levant.
- hamadanensis* (DE LESSE, 1959) (+) – PA: Elburs region.
- larseni* (CARBONELL, 1994) (+) – PA: Levant (Lebanon).
- theresia* SCHURIAN et. al., 1992 – PA: Kurdistan.

**damon**-group (= *Agrodiaetus* s.str.) [PA: Eurasia]

- baytopi* (DE LESSE, 1959) (+) – PA: Elburs region.
- biton* (SULZER, 1776) – PA: Europe (Alps).
- damon* (DENIS & SCHIFFERMÜLLER, 1775) – PA: Europe, Siberia, mountains of S Siberia, N Mongolia.
- iphicarmon* ECKWEILER & ROSE, 1993 – PA: Kurdistan.
- iphidamon* (STAUDINGER, 1899) – PA: Elburs region.
- iphigenia* (HERRICH-SCHÄFFER, 1847) (+) – PA: SE Europe (Balkans), Asia Minor.
- ishashimicus* SHCHETKIN, 1986 – PA: mountains of C Asia.
- juldusa* (STAUDINGER, 1886) – PA: mountains of C Asia.
- nougerae* (DE SAGARRA, 1924) – PA: Europe (Iberia).
- posthumus* (CHRISTOPH, 1877) (+) – PA: mountains of C Asia.
- rovshani* DANTSCHENKO & LUKHTANOV, 1994 – PA: Caucasus region.
- tankeri* (DE LESSE, 1960) (+) – PA: Asia Minor, Kurdistan.

**damone**-group (= *Agrodiaetus* s.l.) [PA: E Europe and Asia]

- altaicus* (ELWES, 1899) (+) – PA: mountains of S Siberia, N Mongolia.
- damocles* (HERRICH-SCHÄFFER, 1844) – PA: E Europe (Crimea, Ural region).
- damone* (EVERSMANN, 1841) – PA: Siberia, mountains of S Siberia, W Mongolia.
- krymeus* (SHELJUZO, 1928) – PA: E Europe (Crimea).
- pljushtchi* LUKHTANOV & BUDASHKIN, 1993 – PA: E Europe (Crimea).
- sibiricus* (STAUDINGER, 1899) – PA: Siberia, mountains of S Siberia.
- walteri* (DANTSCHENKO & LUKHTANOV, 1993) – PA: NW Mongolia.
- fabiani* spec. nov. (+) – PA: Mongolia.

**daphnis**-group (= *Meleageria*) [PA: Europe to Kurdistan]

- buzulmavi* CARBONELL, 1991 (+) – PA: Kurdistan.
- daphnis* (DENIS & SCHIFFERMÜLLER, 1775) – PA: Europe.
- elamita* (LE CERF, 1914) – PA: Kurdistan, Elburs region.
- marcida* (LEDERER, 1872) – PA: Kurdistan, Elburs region.

**dolus**-group s.l. (= *Agrodiaetus*) [PA: Europe, Asia Minor and Kurdistan]

- ainsae* (FORSTER, 1961) (+) – PA: Europe (Iberia).
- antidolus* (REBEL, 1901) – PA: Kurdistan.
- dolus* (HÜBNER, [1823]) – PA: Europe (Iberia).
- feminionides* (ECKWEILER, 1987) – PA: Caucasus region.
- kurdistanicus* (FORSTER, 1961) (+) – PA: Kurdistan.
- menalcas* (FREYER, 1837) (+) – PA: Asia Minor, Kurdistan.
- mofidii* (DE LESSE, 1963) – PA: Elburs region.
- morgani* (LE CERF, 1909) – PA: Elburs region.
- peilei* BETHUNE-BAKER, 1921 (+) – PA: Elburs region.
- phyllides* (STAUDINGER, 1891) – PA: mountains of C Asia.
- phyllis* (CHRISTOPH, 1877) (+) – PA: Asia Minor.
- sennanensis* (DE LESSE, 1959) – PA: Kurdistan.
- vittatus* (OBERTHÜR, 1892) (+) – PA: Asia Minor.

**dorylas**-group (= *Plebicula* s. l.) [PA: N Africa, Europe, Asia Minor and Caucasus]

- armenus* (STAUDINGER, 1871) – PA: Caucasus region.  
*atlanticus* (ELWES, 1906) (+) – PA: NW Africa.  
*dorylas* (DENIS & SCHIFFERMÜLLER, 1775) – PA: Europe, Asia Minor.  
*golgus* (HÜBNER, 1813) – PA: Europe (Iberia).  
*nivescens* (KEFERSTEIN, 1851) – PA: SW Europe.

**eros**-group (*Polyommatus* s. l.) [PA: Asia and SE Europe]

- aloisi* (BÁLINT, 1988) (+) – PA: S Mongolia.  
*amor* (STAUDINGER, 1886) – PA: mountains of C Asia.  
*eroides* (FRIVALDSZKY, 1835) (+) – PA: SE Europe (Balkans), Asia Minor.  
*eros* (OCHSENHEIMER, [1808]) (+) – PA: Europe (Alps, Dinarics).  
*erotides* (STAUDINGER, 1892) – PA: Siberia, mountains of S Siberia, Mongolia.  
*forresti* BÁLINT, 1992 (+) – PA: C Himalayas.  
*menelaos* BROWN, 1976 – PA: SE Europe (Balkans).  
*pseuderos* MOORE, 1875 (+) – PA: Himalayas.  
*venus* (STAUDINGER, 1886) – PA: mountains of C Asia.

**erschoffi**-group (= *Paragrodiaetus*) [PA: C Asia]

- avinovi* (STSHETKIN, 1980) – PA: mountains of C Asia.  
*dagmara* (GRUM-GRSHIMAILO, 1888) (+) – PA: mountains of C Asia.  
*erschoffi* (LEDERER, 1869) – PA: mountains of C Asia.  
*magnifica* (GRUM-GRSHIMAILO, 1885) (+) – PA: mountains of C Asia.  
*pulchella* (BERNARDI, 1951) – PA: mountains of C Asia.  
*superbus* (STAUDINGER, 1887) – PA: mountains of C Asia.

**eurypilus**-group (= *Kretania*) [PA: SE Europe and Crete to C Asia and W. Himalayas]

- csomai* BÁLINT, 1992 (+) – PA: W Himalayas.  
*eumaeon* HEMMING, 1931 (+) – PA: Levant.  
*eurypilus* (FREYER, 1852) (+) – PA: SE Europe (Balkans), Asia Minor.  
*iranicus* (FORSTER, 1938) (+) – PA: Kurdistan, Elburs region, mountains of C Asia.  
*psylorita* (FREYER, 1852) (+) – PA: Europe (Crete).

**glaucias**-group (*Paragrodiaetus* s. l.) [PA: C Asia]

- glaucias* (LEDERER, 1871) – PA: mountains of C Asia.  
*frauvarthianae* BÁLINT, spec. nov. – PA: mountains of C Asia.

**icarius**-group (= *Plebicula* s.str.)<sup>21</sup> [PA: NW Africa, Eurasia]

- abdeliz* (BLACHIER, 1908) – PA: NW Africa.  
*amatus* (GRUM-GRSHIMAILO, 1890) (+) – PA: mountains of C Asia.  
*amurensis* (STAUDINGER, 1892) – PA: Amur region, Korea.  
*anthea* HEMMING, 1932 (+) – PA: Kurdistan, Levant.  
*dalmaticus* (SPEYER, 1892) – PA: SE Europe (Balkans).

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21 *P. icarius* is one of the most common *Polyommatus* species in southern Siberia and Mongolia (BÁLINT: Lycaenids of Mongolia, in prep.). The species is replaced eastward by the large luminous blue *P. amurensis* from the Amur region to the Pacific coast of the Palaearctic region. A morphospecies, *P. abdelaziz*, is restricted to NW Africa, while another, *P. anthea*, occurs from SE Turkey south to Lebanon. *P. amatus* (syntypes examined at BMHN) appears identical with *Lysandra amanda altaishanica* HUANG & MURAYAMA, 1992 and *Lysandra amanda lhasana* MURAYAMA, 1983, but this needs further confirmation from the types of these latter taxa. The *escheri* subgroup is a group restricted to the Mediterranean Basin (records from the Russian steppe are not confirmed, cf. ANIKIN et al., 1993: 117), containing an allopatric morphospecies pair.

*escheri* (HÜBNER, [1823]) – PA: SW Europe.

*icarius* (ESPER, [1789]) – PA: Europe, Siberia, mountains of S Siberia, Mongolia.

**icarus**-group (= *Polyommatus* s.str.)<sup>22</sup> [PA: Eurasia]

*chitralensis* SWINHOE, 1910 (+) – PA: W Himalayas.

*icadius* (GRUM-GRSHIMAILO, 1890) (+) – PA: mountains of C Asia.

*icarus* (ROTTEMBERG, 1775) – PA: Europe, Siberia, mountains of S Siberia, Asia Minor, Caucasus region, Kurdistan, Levant, Elburs region, mountains of C Asia.

*juno* HEMMING, 1933 (+) – PA: Levant (Lebanon).

*kashgarensis* MOORE, 1878 (+) – PA: SW Mongolia, N China.

*turanicus* (HEYNE, 1895) (+) – PA: deserts of C Asia.

**myrrha**-group (= *Sublysandra*) [PA: Asia Minor and C Asia]

*aedon* (CHRISTOPH, 1887) (+) – PA: Kurdistan, Caucasus region, Elburs region.

*myrrha* (HERRICH-SCHÄFFER, [1852]) – PA: Asia Minor.

*myrrhinus* (STAUDINGER, 1901) – PA: Asia Minor, Kurdistan.

**nadira**-group (= *Agrodiaetus* s. l.) [PA: C Asia]

*afghanica* (FORSTER, 1973) (+) – PA: mountains of C Asia.

*baltazardi* (DE LESSE, 1962) – PA: Elburs region.

*delessei* spec. nov. (+) – PA: mountains of C Asia (S Iran).

*nadira* (MOORE, 1884) (+) – PA: mountains of C Asia.

**poseidon**-group (= *Agrodiaetus* s. l.) [PA: Asia Minor and Levant]

*deebi* (LARSEN, 1974) (+) – PA: Levant (Lebanon).

*hopfferi* (HERRICH-SCHÄFFER, 1851) – PA: Asia Minor.

*lycius* (CARBONELL, 1996) – PA: Asia Minor.

*poseidon* (HERRICH-SCHÄFFER, 1851) – PA: Asia Minor.

**poseidonides**-group (= *Agrodiaetus* s. l.) [PA: C Asia, W Himalayas]

*ardschira* (BRANDT, 1938) – PA: Elburs region.

*evansi* (FORSTER, 1956) (+) – PA: W Himalayas.

*florenciae* (TYTLER, 1926) (+) – PA: W Himalayas.

*iphigenides* (STAUDINGER, 1886) – PA: mountains of C Asia.

*melanius* (STAUDINGER, 1886) – PA: mountains of C Asia.

*poseidonides* (STAUDINGER, 1886) – PA: mountains of C Asia.

**semiargus**-group (= *Cyaniris*)<sup>23</sup> [PA: Eurasia]

*antiochenus* (LEDERER, 1861) – PA: Kurdistan, Levant.

*bellis* (FREYER, 1843) (+) – PA: Asia Minor.

*helena* (STAUDINGER, 1862) – PA: SE Europe (Balkans).

*semiargus* (ROTTEMBERG, 1775) – PA: Europe, Siberia, mountains of S Siberia, N Mongolia.

**stoliczkanus**-group<sup>24</sup> (= *Bryna*) [PA: C Asia, Himalayas]

*annamaria* BÁLINT, 1992 (+) – PA: mountains of C Asia.

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22 *P. juno* is sympatric with *P. icarus* in Palestine (BENYAMINI, 1993: 181, footnote). *P. turanicus* is sympatric with *P. icarus* in the Tura region, Kazakhstan. *P. kashgarensis* is sympatric with *icarius* in SW Mongolia ("ssp. *szabokyi*") (based on specimens in HNHM and BMNH).

23 The type of *Aricia monarchus* HIGGINS 1981 was examined (holotype BMNH). The taxon proved identical with the transpalaeartic *P. semiargus*. Therefore, *Aricia monarchus* HIGGINS, 1981 (**syn. nov.**) = *Lycaena semiargus* ROTTEMBERG, 1775.

24 Very recently two interesting taxa were described by the senior author (BÁLINT, 1995a).

*arianus* MOORE, 1865 (+) – PA: W Himalayas.  
*ciloicus* DE FREINA & WITT, 1983 (+) – PA: Kurdistan.  
*dux* RILEY, 1926 (+) – PA: W Himalayas.  
*erigone* (GRUM-GRSHIMAILO, 1890) (+) – PA: mountains of C Asia.  
*everesti* RILEY, 1922 (+) – PA: C Himalayas.  
*fraterluci* BÁLINT, 1995 (+) – PA: W Himalayas.  
*hunza* GRUM-GRSHIMAILO, 1890 (+) – PA: W Himalayas.  
*pierinoi* BÁLINT, 1995 (+) – PA: C Himalayas.  
*stoliczkanus* (FELDER & FELDER, 1865) (+) – PA: Himalayas.  
*sutlejus* MOORE, 1882 (+) – PA: Himalayas.

***transcaspicus***-group (= *Agrodiaetus* s.l.) [PA: Asia Minor, C Asia]  
*afghanistana* (FORSTER, 1972) (+) – PA: mountains of C Asia.  
*aserbeidschanus* (FORSTER, 1956) (+) – PA: Caucasus region.  
*caeruleus* (STAUDINGER, 1871) – PA: Asia Minor.  
*elbursicus* (FORSTER, 1956) (+) – PA: Elburs region.  
*ninae* (FORSTER, 1956) (+) – PA: Caucasus region, Kurdistan.  
*transcaspicus* (STAUDINGER, 1899) – PA: Caucasus region, Kurdistan.

### Hypothetical Branching Diagram of the *Polyommatus* Section (fig. 22)

ELIOT (1973:390) noted that, for him, the male genital aedeagus proved “to be more important in the classification of the subfamily than any other component of the male genitalia” This statement, aside from reflecting ELIOT’s conclusions from his own research, also reflected European tradition, which has consistently turned to the male genital structures for characters in classification (cf. SCOBLE, 1986: 254). Thus, until recently, female genitalia were very rarely investigated.

Recent taxonomic revisions (e. g. HIROWATARI, 1992 and, subsequently, the many papers of the present authors) have shown the importance of female structures, placing lycaenid systematics in a new light. Based on the combinations of data now available from recent revisionary works, we present a hypothetical “branching diagram” for taxa of the *Polyommatus* Section. We base this hypothesis on shared characters inferred to be relatively apomorphic (fig. 22) but avoid employing the word “cladogram” since various workers interpret this word differently depending on whether numerical methods are used or whether “historical” versus “pattern” cladistic methods are applied. The branching diagram is based mainly on male and female morphology since, as noted in subsequent discussion, many elements of polyommata wing pattern appear to reflect adaptive convergence. Our comments below are organized by the numbering of nodes on the diagram. Since this method of discussion does not use numbers to locate specific characters, each numbered entry reviews *both* the synapomorphies uniting taxa at the node and autapomorphies of individual taxa branching from the node.

1) The sister group of the *Polyommatus* Section is the *Nabokovia* Section. In the females, taxa of both sections share long, evertable, genital ductus bursae with sclerotized terminalia. In males, the genital aedeagus is stout, with alulae, and the suprazonal element generally short (or very short) compared with the subzonal element. Considering the distribution of characters in other Polyommata, these characters appear synapomorphic for the two sections. Basally, the two sections show a sagum in the male genitalia, suggesting the outgroup may be the *Pseudochrysois* Section (cf. JOHNSON & BÁLINT, 1995). Considering the sclerotized female terminalia occurring in the *Polyommatus* and *Nabokovia* Sections, female genital terminalia of the *Nabokovia* Section occur in a generally uniform tubular configuration, appearing to be a retained plesiomorphy. In contrast, female terminalia in the *Polyommatus* Section show a broad transition within a more heavily sclerotized

ground plan, viewed here as basically synapomorphic. This ground plan, in basal taxa, shows complex sclerotizations (including “additional components” [apomorphic sensu ELIOT, 1973] like lobes or “wings” in basal taxa) and then appears more or less reduced across the rest of the Section. Assessing such increased reduction as apomorphy is consistent with the view of polarity inferred also for the male’s sagum, and will be discussed in more detail in subsequent entries.<sup>25</sup>

2) Characters in the three known *Echinargus* species suggest a transition series from a plesiotype with large tubular female terminalia and a heavily dentate genital sagum in males (*E. huntingtoni*) to an apomorphic phenotype with elongate tubular female genital terminalia and a reduced sagum in males (*E. isola*). The sister genus of *Echinargus* is *Nabokovia*, which has no male genital sagum and the terminalia less sclerotized (figs. 1, 2). *Nabokovia* shows an obvious adaptive character, namely the discoloration of both genders—male and female being generally brown (see discussion below concerning “The Phenomenon of Discoloration”), a condition most linked to climatic changes during the uplift of the Andes (cf. DENNIS, 1993: 101–127).

3) The reformed *Polyommatus* Section can be divided into two “infratribes”: Pseudolucina (Pseudolucina in the diagram) and Polyommatina (remaining taxa of node 4). The Pseudolucina possess the sagum in males, a trait which, since it appears also in the Nabokovina, is probably a retained plesiomorphy. A basic ground plan in the female genitalia unites the Pseudolucina and, within this infratribe, shows a gradual transformation in sclerotized elements (see details in BÁLINT & JOHNSON, 1995b). The combination of the retained sagum in males but shared derived characters in the female terminalia suggest the Pseudolucina are the more plesiotypic infratribe of the *Polyommatus* Section. By contrast, the Polyommatina, (as noted in more detail in 4, below) are viewed as more apotypic, with shared unique characters in the female genitalia and in the males (particularly the aedeagus). This interpretation of monophyly for the Polyommatina, based on shared derived characters in the genitalia of both sexes and the inferred loss of the sagum in males, is consistent with overall character distributions in the *Polyommatus* Section. An opposite view of polarity would require the genital sagum and complex sclerotizations in the female terminalia to have been independently derived several times.

4) Considering the Polyommatina as viewed in entry 3, two genera (*Aricia* and *Madeleinea*) are united both by unique conditions of the male aedeagus (remarkably slender and curvate in the lateral view, figs. 5, 7) and a particular subtubular sclerotization of the female genitalia (the latter, with lack of any complexifying additional sclerotol features, creating a rather uniform appearance throughout). These conditions are best viewed as synapomorphic for the two genera. In contrast, *Chilades* and the rest of the genera to the left in the diagram have straight (or much less curved) aedeagii in males and female terminalia which are hardly sclerotized, usually with sclerotin limited to the area of the terminal genital opening. These are considered synapomorphic ground plans for the remaining genera of the Polyommatina. Such a view of the Polyommatina, comprised of *Aricia* (*Madeleinea* and *Chilades* and its sister genera) is also consistent with polarities previously inferred for the *Polyommatus* Section herein—various reductions of sclerotol elements being considered generally derived. An opposing view of polarity within the Section would require sclerotol complexifications (sagum in males; lobed or “winged” additional terminal components in females, etc.) be independently derived several times.

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25 Note added in proof: Recent morphological studies of Afrotropical Polyommatina by the senior author resulted an interesting discovery, that the ELIOTIAN *Eicochrysops* Section (monobasic containing only the genus *Eicochrysops* BETHUNE-BAKER, 1924; see ELIOT, 1973: 448–449, text fig. 113 for male genital structures) also possess evertable ductus bursae with sclerotized terminalia, the latter which is tubular but differently structured (see fig. 21). Accordingly, this Section, which is also pending taxonomic revision, must also be considered in the sister group affinity noted here for the Neotropical *Nabokovia* Section.

5) Considering the synapomorphies of *Aricia* and *Madeleina* proposed in entry 4, and conditions in females of the rest of the Section, the condition of sclerotized female terminalia in *Aricia* is best interpreted as more plesiomorphic (a generalized membranous tubular structure, fig. 6), while the unique quadrate configuration typifying *Madeleinea* (unique in the Section, fig 8) is autapomorphic.

6) Regarding the ground plan of the female terminalia (entry 4) which unite *Chilades* and remaining taxa to the left of the diagram, the mainly Palaeotropical *Chilades* show a membranous tubular female structure (fig. 12) more like that of *Aricia* and thus best viewed a retained plesiomorphy. But, in addition, *Chilades* has, in the aedeagal structures referred to in entry 4, a remarkably large supra-zonal element (fig. 11) (cf. figs. 3–4 in NEKRUTENKO, 1984) which must be autapomorphic. All the remaining taxa to the left in the diagram share a very short supra-zonal element in the male aedeagus (the subzonal element always being much longer) and sclerotized parts of the female genitalia which are more uniformly reduced. Consistent with the views of polarity considered so far for the Section these conditions can be viewed as synapomorphic for these taxa.

7) For consistency with the distribution of other characters in the tribe the tubular character of the female genitalia is best interpreted as disappearing in the *Plebejus-Paralycaeides-Agriades-Albulina-Polyommatus* lineage. Accordingly, the membranous and rather strong ductus bursae in *Plebejus-Paralycaeides-Agriades* is probably the most primitive state, with the slender condition in *Albulina* and *Polyommatus* (s. str) relatively apomorphic. *Polyommatus-Albulina* is thus considered the sister group of *Plebejus-Paralycaeides-Agriades*.

8) *Plebejus* and *Paralycaeides-Agriades* share an apparent synapomorphy—a strongly sclerotized supra-zonal element in the aedeagus. In *Plebejus*, however, the male genital supra-zonal element is well developed (just somewhat shorter than the subzonal element), while in *Paralycaeides-Agriades* it is very short. Consistent with the distribution of characters previously reviewed, the condition in *Plebejus* is best considered the more primitive, that uniting *Paralycaeides-Agriades* the more apomorphic.

9) As noted in 8, above, the short but strongly sclerotized condition of the supra-zonal element of the aedeagus appears synapomorphic for *Paralycaeides-Agriades*. Considering the relatively short ductus bursae and platelike anterior lamella in *Agriades*, and the overall view of polarity proposed herein for the Section, the strongly sclerotized anterior lamella in *Paralycaeides* is most likely a retained primitive character.

10) *Polyommatus* and *Albulina* taxa exhibit an apparent synapomorphy in the male genital aedeagus, the supra-zonal element being conspicuously short. The weaker expression of this condition in *Polyommatus* is probably apomorphic relative to more robust and produced supra-zonal states in *Albulina*. Corroborative of this view, in the female genitalia (membranous with extremely reduced sclerotization in the case of both taxa), the almost complete lack of sclerotization near the terminal genital opening in *Polyommatus* can be considered apomorphic relative to the slightly sclerotized condition seen in *Albulina*.

## Discussion

### The Phenomenon of Discoloration in the *Polyommatus* Section

With a worldwide and monophyletic view of the *Polyommatus* Section now available, it is important to explore in more detail the phenomenon of “discoloration” among taxa of this group.

## Significance of Discoloration

In “discoloured taxa” the most striking character typifying sexual dimorphism in the family Lycaenidae is absent—males of discoloured taxa do not show bright upper surface structural coloration (iridescent blue, green, purple or gold) but, instead, have the warm brown pigmental colour typical of females. Historically, difficulty in distinguishing gender among such taxa has led to many taxonomic problems.<sup>26</sup> Further, the biogeographic significance of discoloured taxa has often been overlooked or minimized because many were poorly represented in collections or known only from very limited geographic distributions. Given these circumstances, some discoloured populations (or taxa) were often discounted as insignificant forms or aberrations. With the larger samples available for examination in the present study and its precursors (BALINT, 1991, 1993ab, 1995ab; BALINT & JOHNSON, 1994, 1995a, b, c) we have been able to evaluate the morphological distinctness of many poorly known entities.

Several discoloured species are well known in the western Palaearctic region. One of the most striking is *Plebejus maurus* which is restricted to a few high montane localities in the Atlas Mountains of NW Africa. On the Iberian Peninsula another example of an apparently endemic discoloured species is *Aricia morronensis*. In addition, the Iberian region has several endemic discoloured “*Agrodiatus*” species. Because of a wider knowledge of western Holarctic species among lepidopterists, these discoloured species have been the most familiar.

By contrast, relatively large numbers of discoloured populations (and taxa) occur in parts of Asia where the “normal” polyommata fauna is also very diverse. In the west, numerous taxa of discoloured polyommata are known from the Caucasus mountain region, the mountain ranges of south-eastern Anatolia, and in the Lebanon and Elburz mountain ranges. Eastward, numerous additional locations of discoloured taxa occur in the high mountains of Inner Asia and the Himalayas of Tibet. Conspicuous to the admixture of discoloured taxa in these regions is the fact that many genera and species groups are represented. Also notable is the fact that most of these discoloured taxa occur in geographically isolated populations generally peripheral to the overall distributions of their respective species groups. Further, such distributions generally coincide with hostile climates typifying extremes of altitude or latitude, a situation also mirrored by discoloured polyommata of the New World. This generality, along with the fact that morphologies of isolated discoloured taxa are often highly autapomorphic, suggests that, overall in the *Polyommatus Section*, (i) discoloration is a derived condition and (ii) discoloured endemics (often greatly similar in external features) have generally arisen through adaptive convergence.

The present study has shown that morphological distinctiveness in discoloured taxa (historically well-established in the few discoloured western Palaearctic taxa) is borne out in the panoply of discoloured taxa characterizing the eastern Palaearctic and New World. Since the morphologies of most discoloured taxa support their rank as species, discoloration appears to be a significant product of speciation in the *Polyommatus Section*, one meriting ongoing analysis of its historic and geographic patterns. This contrasts previous views of discoloration, wherein such specimens were either left taxonomically unresolved in systematic studies and collections or simply treated as “rare” forms of certain, or unspecified, taxa.

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26 This led to the historical misinterpretation of several taxa, e. g. BUTLER (1881) thought that the type specimens of “*Scolitantides andina*” were females. Therefore he believed that the blue coloured specimens collected with *andina* represented the males. A century passed until the identity of these specimens was re-examined and the material studied by BUTLER served as the type series for the description of *Cherchiella argentina* BALLETO, 1993 and *Pseudolucia sirin* BALINT, 1993.

## Vicariant Patterns and Normal and Discoloured Polyommatini

Given the consistency of worldwide vicariant patterns, it is likely that the taxonomic and geographic distributions of discoloured and normal polyommata taxa reflect patterns in certain other groups of biota. Among lower taxa (species groups, species and subspecies) such patterns most likely reflect a combination of (1) longer term (upper Cenozoic) geologic and climatological isolating mechanisms and (2) more recent, Holocene, factors in which man and herbivores have played a major role.

Long term processes of geographical and/or climatological vicariance are well-documented in literature treating the biogeography of the upper Cenozoic era (among others, see BRYSON, BAERRIS & WENDLAND, 1970; CHANEY, 1936; CHARLESWORTH, 1957; CUSHING & WRIGHT, 1967; LIVINGSTONE & SHREVE, 1921; MARTIN, 1958; WELLS, 1970; WRIGHT & FREY, 1965). These larger forces in time and space undoubtedly underlie the ranges of various monophyletic groups within the *Polyommatus Section*. For instance, components of Laurasian distributions occur in *Aricia* and the *idas* group of *Plebejus*, Laurasian and north African patterns typify the *pylaon* group of *Plebejus* and the *dorylas* and *icarius* groups of *Polyommatus*. Beringian distributions are found among the *aquilo* group of *Agriades*.

However, as is well known, even upon this "larger stage" of macro-isolating mechanisms other disjunctive forces are much more localized and work within relatively short periods of geologic time. Examples are glacial, pyroclastic, pyrographic, edaphic, or eustatic factors (see MASON, 1946; RAND, 1948; SHIELDS, 1996; STEWART, 1952, 1956). In the *Polyommatus Section* there are significant numbers of species with distributions influenced by past glacial topography (the eastern Palaearctic *ellisi* and *sikkima* groups of *Agriades*, the *damone* and *erschoffi* groups of *Polyommatus*, Andean fragments within *Madeleinea*, *Nabokovia* and *Paralycaeides*, etc.). Coastal isolates, reflecting eustatic changes, occur in Palaearctic *Plebejus idas* subspecies and in Neotropical *Pseudolucia*. Disjunctive distributions reflecting pyrographics of the last interglacial period occur among grassland polyommata like the *icarioides* group of *Aricia*.

Some discoloured taxa, typically representatives of taxonomically complex groups referred to in the present paper as "superspecies" (e. g. *agestis*-complex, *ripartii*-complex and *eumedon*-complex) appear to have distributions which reflect more recent biogeographic forces. Distributions of such polyommata are coincident with events of the Holocene landscape—specifically, the history of land use by vast herds of herbivores and the activities of man.

Biogeographic activities of the Holocene period have a significant scientific literature (among others, BUTZER, 1971; MARTIN & WRIGHT, 1967; SAUER, 1950, 1952, 1956; SELLARDS, 1952; STEWART, 1952, 1956; THOMAS, 1956; WENDORF & HESTER, 1962). Large scale disturbances by man and herbivores have effected continual expansion and contraction of forest, steppe, and arid grassland mosaics in comparatively recent periods of time (DORT, 1970; GLEASON, 1913; HOFFMAN & TABER, 1967; HULTÉN, 1937; HUMPHREY, 1958; MARTIN, 1958; SIMON, 1997; WELLS, 1970). Early interactions between man and wandering herds of foraging mammals are evident in the cave drawings of Eurasian man (GRAZIOSI, 1960; BREUIL, 1970) and oral traditions recorded among Holarctic tribes which entered the New World (BRYAN, 1965; SELLARDS, 1952; WENDORF & HESTER 1962; WORMINGTON, 1957). Effects by man on the landscape escalated with the proliferation of farming and domestic herding and these activities led to the complete disclimax of some temperate biomes in periods as short as a few to one hundred years (GEERTZ, 1963; GLEASON, 1913; GREGG, 1954; KLEIN, 1969; SAUER 1950, 1956; SIMON, 1997; STEWART, 1952; THOMAS, 1956; WEAVER & ALBERTSON, 1956; WELLS, 1970). Given the dominance of agriculture over the modern landscape, and its coincidence with former natural grassland communities (see any map projection concerning "Agriculture" or "Food" in a geographic Atlas), one cannot understate the effects of very recent forces of the distribution of non-domestic grassland herbivores. Yearly expansions and contractions of some ranges are already

well-known (see, for instance, Nearctic *Echinargus isola* as reflected in any popular butterfly guide [e.g. OPLER & MALIKUL, 1992]). Such yearly expansions even require adjustment in our distribution maps (fig. 23).

The botanical literature documents an important “two-tier” interplay in the interactions of older and more recent factors influencing biotic distributions. Smaller scale vicariations (typifying local regions or biomes) mirror, or actually recapitulate, larger scale actions which have occurred (or are simultaneously occurring) over far vaster expanses of time and space (DORT & JONES, 1968; HUMPHREY 1958; LIVINGSTONE & SHREVE, 1921; WEAVER & ALBERTSON, 1956). An example of primary significance to grassland herbivores is the short grass disclimax and its relation to agricultural interference by man (concerning the Holarctic see WEAVER & ALBERTSON, 1956; DORT & JONES, 1968). Grassland disclimax (be it of prairie, plains, steppe or paramo, etc.) is important to understand because typical of its end result, either by ongoing degradation or substitution of a domestic flora, is a “post-climax” biota. In post-climax, although random vestiges of the original flora may survive (or even thrive in small areas), ecological niche destruction is so pervasive that few (if any) of the originally associated herbivores usually survive (WEAVER & ALBERTSON, 1956).

Replacing the original biota is a new one,<sup>27</sup> usually far less diverse biotically, in which smaller numbers of opportunistic species may thrive. For this smaller diversity of species disclimax is not negative and, with selection favoring pioneer and replacer plants, certain polyommata may also thrive and expand. Fragmentation of floras affects dynamics of foodplant utilization in butterflies. DOWNEY (1962), DOWNEY & FULLER (1961) and DOWNEY & DUNN (1964) documented shifts of larval foodplant usage in groups of North American *Aricia* in very short periods of years. Similarly, SHIELDS (1996) provides a rich list of contexts in which residence within widening or shrinking ecological niches could provide opportunities for explosive evolution. It is evident that man’s massive alteration of the modern landscape offers a finely hewn mechanism for vicariance, one from which new lineages may be initiated and thrive. This is well demonstrated and documented in the Carpathian Basin by the representatives of *Plebejus sephirus* (c.f. BALINT, 1991). Where butterfly herbivores adapt to rather uniform and widespread distributions characterizing post-climax or domestic floras, opportunities for gene flow, not isolation, are provided.

Biogeography of the *Polyommatus Section* requires an appreciation of both long term and recent biogeographic events, balancing a search for tectonic generalities, assessment of longer term Cenozoic factors, and influences of the more recent Holocene landscape. Some studies in Paleoecology have traced biogeographic patterns through monitoring geographic distributions of insects (ROSS, 1970; ROSS & HAMILTON, 1970) or other invertebrates (TAYLOR, 1965) but this has not been a prolific area of published research. Concerning polyommata, a challenge remains to identify and elaborate their component patterns among normal and discoloured taxa and link these patterns to influences which may put species at risk. Unfortunately for scientists, many discoloured taxa are poorly known or from areas infrequently collected. However, the present paper calls attention to the biogeographic significance of discoloration. From what we now know of total numbers of discoloured taxa in the the Polyommata, the frequency of this convergent phenomenon in the Tribe is remarkable.

### **Distribution of Discoloured Taxa (Table 2)**

In the Afrotropical region there is only a single genus in the *Polyommatus Section*—*Chilades*, a genus far more widespread in the Oriental realm. With regard to discoloration, all the African taxa of *Chilades* are “normal” and only one of these, most likely the result of a relatively recent dispersion, reaches the Palaearctic. This is *Chilades trochylus* which, from a widespread central Asian distribution, enters the Palaearctic in the Arabian region.

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27 “Noosphere” sensu TEILHARD DE CHARDIN (1955, 1959).

The *Polyommatus Section* is relatively weakly represented in the Oriental region. The above-mentioned species, however, (*Chilades trochylus*) is very common in the arid regions of Central Asia along the southwestern edge of the Himalayas. Notably, *C. trochylus* has a discoloured sister species in the Himalayas, *Chilades putli*.<sup>28</sup> Also, there are a number of additional discoloured species, each poorly known, in the highest regions of the Himalayan region (e. g. *Agriades ellisi*, *Aricia astoricus*, *Plebejus baroghila*, etc.). Unfortunately, the current paucity of data concerning these species makes it impossible to comment on their overall zoogeographic spread. Of great interest, however, is that fact that the biotopes they inhabit appear to be those with clear Palaearctic affinities.

In the Nearctic region there is a remarkable discoloured polyommatine species, *Aricia neurona*, which is endemic to California. In the traditional view, its occurrence has been viewed as resulting from part of the recent Nearctic polyommatine fauna arriving from Asia (cf. SHIELDS, 1996: 80). However, the assignment of this species in *Aricia* elicits even further interest, because *Aricia* has both Palaearctic and Neotropical affinities.

In the Neotropical region discoloured taxa become very obvious. All the known representatives of *Paralycaeides* are discoloured. One, *P. vapa*, is widely distributed from southern Peru south to Patagonia along the eastern side of the Andes Mountains. The genus *Madeleinea* contains a discoloured high Andean taxon, very recently discovered—*M. bella* BÁLINT & LAMAS. Another, *M. moza*, shares the wider general distribution of *P. vapa*. It is likely these species may expand their ranges because of the widespread and recent aridization taking place in many upland areas throughout the neotropics (see, for instance, BENYAMINI, 1995). Some species of Neotropical polyommatine, paralleling some of the “blues” from the Old World, are gaining from the results of agriculture (where disturbed areas are opened for weedy “early invader” or “replacer” plants). Table 3 notes exemplary polyommatine taxa whose ranges appear to be expanding with man’s alteration of the environment.

JOHNSON (1986) documented this phenomenon in North America and BENYAMINI (1995) has noted examples in the Andes and austral regions of South America. Such expansions, usually tied to a small percentage of insect herbivores utilizing plants which become more common or widespread with habitat disruption, starkly contrast the many biotic losses usually associated with habitat destruction. In the relatively “coarse-grained” ecologies of North America, where overall biotic diversity is less than in “fine-grained” ecologies like the tropics, micro-vicariations due to habitat destruction tend to cause fewer overall taxonomic problems, at the most bringing up questions of subspecies or complexes within superspecies. However, in South America, where much of the temperate upland biota appears to have evolved from an already diverse lowland tropical fauna, there can be little doubt that the frequency of unique isolates (as with many discoloured polyommatine populations in genera such as *Pseudolucia*, *Madeleinea* and *Paralycaeides*) creates problems regarding evaluation of taxonomic rank. For instance, BENYAMINI (1995), precisely in groups herein noted as increasing their dispersion in response to aridization, records distinctive populations of *Madeleinea* separated only by short distances across South America’s continental divide. In general, in North American or European habitats, one would not expect populations so geographically close, and ecologically similar, to contain such disparate congeners. However, a similar phenomenon exists in several semiarid and arid regions of Asia in some *Polyommatus* species groups.

It is of particular interest, considering the affinities of discoloured polyommatine taxa in the neotropics, that although all the known species of *Nabokovia* (the entirely high Andean genus of the *Nabokovia Section*) are discoloured, the species of its pan-American sister genus, *Echinargus*, are “normal” Yet, if one considers the overall ranges and diversity of these genera in light of our view that discoloration in a convergent character reflecting geographic isolation within similarly hostile climates, *Echinargus* differs generally from *Nabokovia* in being a genus with species of widespread distribution occupying long established, and coarse-grained, ecologies.

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28 Most probably, *C. putli* is a synonym of *C. trochylus*.

Table 2

Discoloured taxa recognized in the reformed *Polyommatus Section* listed in alphabetical sequence (their biogeographical regions indicated in brackets) (colour plates 1–4)

<i>Agriades dis</i> (PA)	<i>Agriades janigena</i> (PA)
<i>Agriades ellisi</i> (PA)	<i>Agriades luanus</i> (PA)
<i>Agriades franklinii</i> (NA)	<i>Agriades rusticus</i> (NA)
<i>Albulina amphirroae</i> (PA)	<i>Albulina iris</i> (PA)
<i>Albulina felicis</i> (PA)	<i>Albulina rutilans</i> (PA)
<i>Albulina gaborronkayi</i> , spec. nov. (PA)	<i>Albulina younghusbandi</i> (PA)
<i>Albulina hanna</i> (PA)	
<i>Aricia agestis</i> (PA)	<i>Aricia kogistana</i> (PA)
<i>Aricia allous</i> (PA)	<i>Aricia mandschurica</i> (PA)
<i>Aricia artaxerxes</i> (PA)	<i>Aricia morronensis</i> (PA)
<i>Aricia astorica</i> (PA)	<i>Aricia mylitta</i> (PA)
<i>Aricia bassoni</i> (PA)	<i>Aricia myrmecias</i> (PA)
<i>Aricia chinensis</i> (PA)	<i>Aricia neurona</i> (NA)
<i>Aricia cramera</i> (PA)	<i>Aricia persephatta</i> (PA)
<i>Aricia crassipuncta</i> (PA)	<i>Aricia privata</i> (PA)
<i>Aricia eumedon</i> (PA)	<i>Aricia timida</i> (PA)
<i>Aricia inhonora</i> (PA)	<i>Aricia transalaica</i> (PA)
<i>Aricia issekutzi</i> (PA)	<i>Aricia vandarbani</i> (PA)
<i>Chilades putli</i> (PA)	<i>Chilades trochylus</i> (PA)
<i>Chilades minuscula</i> (AFR)	
<i>Madeleinea bella</i> (NT)	<i>Madeleinea vokoban</i> (NT)
<i>Madeleinea moza</i> (NT)	
<i>Paralycaeides hazelea</i> (NT)	<i>Paralycaeides shade</i> (NT)
<i>Paralycaeides inconspicua</i> (NT)	<i>Paralycaeides vapa</i> (NT)
<i>Plebejus baroghila</i> (PA)	<i>Plebejus pilgram</i> (PA)
<i>Plebejus firuskuhi</i> (PA)	<i>Plebejus themis</i> (PA)
<i>Plebejus lucifera</i> (PA)	<i>Plebejus vogelii</i> (PA)
<i>Plebejus lucifuga</i> (PA)	
<i>Polyommatus admetus</i> (PA)	<i>Polyommatus frauartiana</i> , spec. nov. (PA)
<i>Polyommatus afghanicus</i> (PA)	<i>Polyommatus galloi</i> (PA)
<i>Polyommatus alcestis</i> (PA)	<i>Polyommatus humdeasae</i> (PA)
<i>Polyommatus aroaniensis</i> (PA)	<i>Polyommatus interjectus</i> (PA)
<i>Polyommatus avinovi</i> (PA)	<i>Polyommatus iranicus</i> (PA)
<i>Polyommatus ardschira</i> (PA)	<i>Polyommatus marcida</i> (PA)
<i>Polyommatus budashkini</i> (PA)	<i>Polyommatus mithridates</i> (PA)
<i>Polyommatus csomai</i> (PA)	<i>Polyommatus nephohiptmenos</i> (PA)
<i>Polyommatus demavendi</i> (PA)	<i>Polyommatus paralcestis</i> (PA)
<i>Polyommatus eumaeon</i> (PA)	<i>Polyommatus pelei</i> (PA)
<i>Polyommatus eurypilus</i> (PA)	<i>Polyommatus psylorita</i> (PA)
<i>Polyommatus exuberans</i> (PA)	<i>Polyommatus pulchella</i> (PA)
<i>Polyommatus fabressei</i> (PA)	<i>Polyommatus ripartii</i> (PA)
<i>Polyommatus feminioides</i> (PA)	<i>Polyommatus valiabadi</i> (PA)
<i>Pseudolucia andina</i> (NT)	<i>Pseudolucia neuqueniensis</i> (NT)
<i>Pseudolucia chilensis</i> (NT)	<i>Pseudolucia oligocyanea</i> (NT)
<i>Pseudolucia magellana</i> (NT)	<i>Pseudolucia parana</i> (NT)

Table 3

In alphabetical order, genera and species, along with generalized geographic regions, where habitat interference by man appears to be creating more favorable conditions for range expansion of certain polyommataines.

*Aricia acmon* — Nearctic region  
*Aricia agestis* — Palearctic region  
*Chilades cleotas* — Oriental region  
*Chilades kedonga* — Afrotropical region  
*Chilades trochylus* — Palearctic region  
*Echinargus isola* — Nearctic region  
*Madeleinea moza* — Neotropical region  
*Paralycaeides vapa* — Neotropical region  
*Plebejus argus* — Palaearctic region  
*Plebejus idas* — Holarctic region  
*Pseudolucia chilensis* — Neotropical region  
*Pseudolucia lyrnessa* — Neotropical region  
*Polyommatus icarus* — Palaearctic region

### Summary and Comparisons to Other Faunas

Contrasting rather anecdotal attention given by previous literature to the phenomenon of discoloration in the Polyommataini, it appears now that lack of dorsal iridescence is a widespread adaptive and convergent character within the tribe in general and the *Polyommatus Section* in particular. Discoloration occurs in all the species groups of the *Polyommatus Section* as well as throughout the Section's distribution. It is also prominent in the sister group, the *Nabokovia Section*. Dorsal discoloration occurs both in scattered taxa of some lineages (where it coincides with high elevation and cold and arid conditions) and universally in others, where extreme upland or cold and arid habitats characterize all the taxa. Reduced size, and certain odd wing shapes, also appear commonly among taxa with discoloration. With discoloration now recognized as a widespread phenomenon among the Polyommataini of certain habitats, more attention should be given to the distributions of other characters in these taxa which, hitherto, have often escaped attention because of the paucity of literature on high upland or remotely distributed species.

There is a parallel to the phenomenon of discoloured polyommataine taxa in the fauna of Eumaeini (the "hairstreak butterflies") occurring in extreme upland and cold/arid regions of the Andes Mountains and austral areas of South America. The prevalent historical view, that polyommataine and eumaeine faunas in such regions were depauperate (LARSEN, 1991; DESCIMON, 1986), has been reflected in the overall biogeographic assessment of these faunas and regions. However, from data now available, these old views appear now to have resulted primarily from sampling error (JOHNSON, 1990, 1992; BÁLINT & JOHNSON, 1995a). In the past, the occurrence of generally similar, dull or cryptic, external facies among various high altitude or austral Lycaenidae led to the assumptions that little diversity was present. We see now, however, that a panoply of morphological features underlying these common external facades. Even to the trained worker, the brown upper surfaces and white or silver spotted under surfaces of such polyommataine genera as *Madeleinea*, *Paralycaeides*, or even certain *Itylos*, can cause great confusion. In the hairstreak butterflies, taxa from infratribes as disparate as Strymonina and Thecloxurina (both with many brilliant coloured, exotic looking, lowland species) require dissection to properly assign (even to infratribe) their small, dull, and cryptic "elfin"-like high montane sister taxa. If mimicry enters the picture, as suggested with orange-patched polyommataines (BENYAMINI, 1995) or orange-coloured high elevation hairstreaks (JOHNSON, 1990, 1992; JOHNSON, MILLER & HERRERA, 1991; BENYAMINI & JOHNSON, 1996) even specialists may have trouble distinguishing genera by external features. Yet, beneath the surface, nothing could be more different

than the morphologies of polyommata species like orange *Pseudolucia collina* and its look-alikes (BÁLINT & JOHNSON 1995d; BENYAMINI, 1995) or orange thecline look-alikes like *Penaincisalia aurulenta* JOHNSON and *Shapiroana matusiki* JOHNSON (JOHNSON, 1992). Morphological elaboration of these faunas, coupled with recent contributions concerning field biology (BENYAMINI, 1995) documents, without doubt, that a much higher diversity is present than formerly anticipated (SHAPIRO, 1994). Thus, with this increased documentation of diversity, the need has arisen to for a complete reelaboration of the genera and species diversity of a reformed *Polyommatus Section*, as in the present paper.

### **Area Distributions of the Reformed *Polyommatus Section* (fig. 23)**

Study of the area diagram of the present paper (fig. 23) reveals a rather tectonically coherent pattern for the group, beginning with a total modern distribution embracing that of all of ancient Pangaea except Australia. However, one must caution from the beginning that grassland polyommata are likely poor tests for retrieving distribution patterns of tectonic significance because they are such good dispersers. "Dispersion", that is, natural expansion of a range to fill a compatible ecological space (PLATNICK, 1976) (as opposed to "Dispersal", dispersal across a geographic barrier) is even a more apt tendency in blues of the *Polyommatus Section* as apparently evidenced by the continental distributions of many of the taxa and groups as well as the frequency of widespread distributions across closely clustered continental areas. Although an overall Pangean distribution appears notable, with subsequent Gondwanian and Laurasia components, lack of any distinct *primary* Gondwanian versus Laurasia components suggests interpretation of the total distribution in light of early plate tectonics is probably weak. This view is supported by the lack of distributions in primary Gondwanian areas like Australia, and secondary Gondwanian areas like India. What appears most likely are late Cretaceous and Cenozoic events, with the Section expanding widely among the closely adjacent continental areas generally typifying that time period.

Similar transcontinental distributions, including Eurasia, Africa, North America and certain parts of South America typify the first four basal nodes of the ingroup. The outgroups show a reduced distribution exclusive to the Neotropical Realm. This reduction of South American distributions also typifies initial nodes of the ingroup. Isolation of the South American fauna, seen in numerous genera of the section like *Madeleinea*, *Pseudolucia* and *Paralycaeides*, probably reflects two factors: (1) South America's relatively more isolated Cretaceous position compared to Africa (the latter closely abutting another major land area, Eurasia) and (2) the fact that most of the South American polyommata fauna occupies the more temperate biomes of the Andes and austral regions attributable to Cenozoic (Eocene, Miocene) Andean uplift. As BÁLINT & JOHNSON (1995a) have previously noted, the apparently autochthonous character of many of the South American polyommata genera (*Polyommatus Section* and otherwise) suggests an uplifted origin from lowland ancestors restricted to the early neotropics. In fact, only two genera (*Madeleinea* and *Paralycaeides*, both of the *Polyommatus Section*) have morphological characters suggesting some Holarctic affinity (see BÁLINT & JOHNSON, 1994, 1995a, c).

African distributions in the *Polyommatus Section* appear heavily influenced by the faunas of adjacent Eurasia, again a Cenozoic phenomenon. North African elements reflect the Palaearctic affinities typical of many groups of biota. More nuclear African taxa reflect more lowland tropical affinities than their South American counterparts and show much wider pan-African distributions. This is consistent with the less broken topography of Africa in general. Distribution patterns in the Section most consistent with tectonic events are those comprised of Laurasian elements. These include Holarctic distributions at the generic level, with species groups showing various Holarctic, Palaearctic, Nearctic, or Beringian distributions. This is consistent with our previous discussion of "discoloration" in the Section and Cenozoic and Holocene events.

## Systematic Methods and Views of Diversity

Following our notes above concerning the comparative biology and biogeography of polyommataines of the *Polyommatus Section*, special comment is warranted on the relatively recent "explosion" of descriptive work concerning these, and other, lycaenid butterflies worldwide. This recent taxonomic work has resulted in a substantial increase in species numbers and it is important to understand if this is due primarily to more fine-grained taxonomic methods used, or whether, in fact, previous views of diversity in these groups have been deficient.

Character-based (or alpha taxonomic) methods used by us and others (BÁLINT & JOHNSON, 1994, 1995a–d; BÁLINT & LAMAS, 1994, 1996; BENYAMINI, BÁLINT & JOHNSON, 1995a–c) in developing current views of the *Polyommatus Section* need to be distinguished from certain other taxonomic methods. These include: the "typology" of the old "Empirical School" of taxonomy (which is still, unfortunately, the basis of most common usage for the Lycaenidae and many other butterflies) (see CRAECRAFT, 1974; JOHNSON & QUINTER, 1983); "biological species" (with its inherent operational problems), and "morphospecies" (which have very strict definitions within certain phylogenetic methods of systematics).

### Character-based Taxonomic Methods

Increases in species numbers often occur when species categories are construed from (1) consistencies of multiple shared characters (both external and internal) and (2) comparison of these to the same constellations of characters in type specimens. Increases in lycaenid, riodinid and hesperid species numbers have recently occurred because (1) such methods have not had wide previous use and (2) specimens representing many farflung localities (either in neglected old museum material or from recent field collections) have often been studied only recently.

However, taxa resulting from such character-based taxonomic studies are not necessarily "morphospecies" per se, as the latter are often very strictly defined in different phylogenetic approaches to systematics. BAUM & DONOGHUE (1995) have recently distinguished two kinds of phylogenetic methods (or phylogenetic inference)—one "character-based" and one "history [i. e. ancestry]-based" Views of character *ontology* (e. g. what characters mean) differ between the two methods. In the character-based method ("pattern cladistics") branching diagrams claim to express only characters; in the history-based method ("evolutionary phylogenetics") branching diagrams claim to express history or lineage. A fine-grained alpha taxonomic approach, as used by the present authors and some of their colleagues, doesn't aim specifically at either one of these methods. Rather, it produces a data base which is adaptable for character-related inference, irrespective of what ultimate method of inference is preferred. Such data can be adapted to the needs of different "phylogenetic" approaches just as taxa derived from the same methods can be used to predict "biological" species whose biology can then be studied in the field.

### Biological Species

The biological species is a fundamental concept in evolutionary biology but one whose operational application has been fraught with problems. Both the veracity and utility of this measure have been widely questioned, or even discredited, generally because of problems concerning (1) non-testability, and (2) "interbreeding"'s fallability regarding predicting historical relationships or lineages (BAUM & DONOGHUE, 1995; ROSEN, 1979; CRAECRAFT, 1974). At least among systematists interested in history-based inference, the biological species is no longer seen as a useful methodological tool (for the shortest and perhaps most available review of this matter as regards Lepidoptera, see COLLINS, 1991 and 1996). Operationally, however, and perhaps more important here, it should be emphasized that, for Polyommataini and Theclinae, we simply do not have the kinds of biological and/or ecological data necessary for a discussion of relationships in this context. In fact, such data are available for very few Lepidoptera (COLLINS, 1996). Measures of reproductive compatibility have proven extremely useful regarding concepts of taxonomic relationships (FRIEDLANDER, 1987; OLIVER, 1972, among others), and understanding primary versus secondary intergradation (PLATT, 1975, 1983; PLATT & BROWER,

1968; REMINGTON, 1958, 1968; among others) in certain relatively non-speciose butterfly groups. However, such data are generally not available for extensive application to speciose groups of Lycaenidae, Riodinidae or HesperIIDae in tropical regions. Realizing this, various authors have pointed to fine-grained alpha taxonomic techniques as a method of predicting or “red-flagging” entities that should be studied biologically (AUSTIN & JOHNSON, 1995, 1996 & in press; JOHNSON & SOURAKOV, 1993; JOHNSON & KRAUSE, in press).

## Typological Species

The word “typology” reflects the 1950’s “Empirical School” of taxonomy and refers to the choice of one (or several) arbitrary characters, usually externally obvious, to distinguish a species (CRAECRAFT, 1974; JOHNSON & QUINTER, 1983). The method derives from the diagnostic format of traditional taxonomy where an initial “Diagnosis” entry summarized one or two key characters to be used for identifying the described taxon. We will return to this topic again in more detail because typological identification still dominates much of Lepidopterology, and its use has certain deleterious effects concerning recognition of actual species diversity. There is a close relationship between typological views of taxa and the problems modern systematics has clarified concerning “grades”. A grade is a set of specimens generally alike in certain arbitrary characters but differing greatly otherwise (for example in morphology, sexual dimorphic patterns, or secondary sexual characters) and thus not actually conspecific (or even congeneric). When grades are viewed as “species” (1) actual diversity may be hidden within the grade and (2) variant sets of specimens within the grade are arbitrarily considered “subspecies”, “forms” or “races” of the grade “species” without further investigation or emphasis on additional characters. Typology of this sort typifies certain creationist views of species (see D’ABRERA 1995: ix, 1248) wherein the key diagnostic characters are also construed as reflecting the identity, “type” or “kind” created, with all variants constituting genetic “reduction” of the original species to subspecies, forms or races. Typological views of butterfly diversity must be mentioned because they still dominate much of the popular literature on butterflies and this popular literature is still widely used for museum curation, field identification, and assessments of biogeography.

## Species Methods and Species Numbers

If fine-grained taxonomic approaches lead to increases in species numbers, does this mean that the use of “biological species” would result in fewer new species? We think not. Firstly, studies of life histories and ecology have tended to increase, not decrease, appreciation of species numbers in the Lepidoptera (cf. KUDRNA, 1996: 16). Secondly, lepidopterists must recognize that the only reasons we have had relatively small numbers of species in the Polyommata and Theclinae prior to recent “explosions” of species numbers are:

- (1) sampling error, and
- (2) the fact that many “species” in the historical common usage for tropical Lycaenidae have simply been “grades”. As noted previously, a “grade” is a set of specimens misconstrued as representing a single species. Such sets of specimens may appear externally much alike but, when studied in more detail (with reference to additional characters like details or consistency of wing pattern, genitalia, tergal morphology, internal and external secondary sexual elements, etc.) are exposed as having no systematic coherence. “Grades” of specimens are often not conspecific and, particularly if initially misdiagnosed as to gender, sometimes not even congeneric. This fact is well recognized in studies of moths and skippers (BURNS, 1987, 1989, 1990, 1992, 1994a, 1994b) yet there appears to be a reluctance in accepting its reality among other butterflies. Examples are apparent in many museum curations of the Lycaenidae and Riodinidae with diverse specimens grouped by the major characters of a few historical taxa and perusal of such sets revealing panoplies of different wing pattern details, locations and sizes of secondary sexual characters, etc. Biological study of “grades” often suggests reasons for misleading superficial similarity—for instance, adaptive convergence or mimicry rings like those suggested recently by BENYAMINI (1995) among orange Polyommata and Theclinae based on a toxic *Cuscuta*-feeding model.

## How Typology in Common Taxonomic Usage Affects Views of Diversity

Reluctance to “look beneath the surface” in butterflies could stem simply from a desire for taxonomic stability and simplicity (EHRlich & MURPHY, 1983). However, we think the problem is more complex—on one hand harmlessly “cultural” but, on another, cloaking some very negative consequences.

### Assumptions Concerning Common Usage

Many lepidopterists seem to equate the relatively low species numbers typifying lycaenid or rioidinid common usage with what they imagine *would be true* if the actual numbers of “biological species” were known. Reminiscent of gradualist paleontologists (who imagined that “gap” or “missing link” taxa would be discovered connecting the known fossil taxa) employment of omnibus species in the common usage for lycaenid and rioidinid butterflies necessarily presupposes that, aside from key diagnostic characters, all superficial (or other) differences between specimens assigned to such “species” simply represent taxonomically insignificant variation. Such predelection may explain why some lepidopterists either ignore, or argue strongly against, descriptions of new species from the grades of conventional taxonomic usage even if numerous non-superficial characters are shown to be distinctive. For them, departure from the common taxonomic usage constitutes arbitrary taxonomic “splitting”

For instance, a collections-based lepidopterist (known by us to be a very reputable and conscientious worker) wrote to us recently (anonymous, in litt.) that, even with consilient differences in characters as diverse as external and internal secondary sexual elements, genitalia from both sexes, tergal morphology and sexual dimorphism, departures from common usage were “difficult to accept” Given the sheer number of additional characters showing that certain grade species are actually para- or polyphyletic, we can only imagine that, for this worker, “key” characters from the traditional typological taxonomy are so obliging that all departures must constitute simply “variation” On the other hand, some (particularly taxonomically trained) workers value the fine-grained taxonomic approach and we find many field-based workers often “excited” to investigate the biologies of recently described species. They often respond quickly with ecological and biological data supporting the distinction of such taxa (see BENYAMINI, 1995: 47).

Lepidopterists having difficulty with the recent proliferation of names (or changes of binomial combinations) in Lycaenidae, Rioidinidae and Hesperidae are often workers more familiar with the well-studied (and thus historically more stable) nymphalid, papilionid or pierid families. They can rightly believe that common taxonomic usage for these latter groups is sound; however, they also appear to want to tag every specimen of the lesser known groups with some available name (no matter how disparate the interpretations of these names may be or how those interpretations relate to types).

### Different “Common” Usages

Often, lepidopterists are not aware that they have chosen different sets of arbitrary external characters to identify the same taxon (one perhaps using wing pattern only, one wing pattern plus reference to wing tails, scent brands, etc.). Consequently, correspondence, locally published faunal lists, and collection curations may all differ in the application of names (MILLER, 1996). Some museums respond to specialists’ inquiries concerning undetermined specimens that all their holdings have been (in the words from one recent letter) “readily identified with available names” To the extent that such identifications are inaccurate (since it is apparent when reference to types has not been employed) the practice actually inhibits data retrieval. Collections marking questionable specimens as “unidentified” or, if critically studied, “spec. nov.” (as at the BMNH) have far more utility for the inquiring worker than collections where all specimens are “identified”

### Problems Regarding Types

Taxonomic problems resulting from lack of reference to types are straightforward. Types are often not dissected, lack lectotype or neotype designations, or (very often) are simply ignored. Books like

D'ABRERA'S 1995 photofolio of Neotropical Lycaenidae in the BMNH generally do not differentiate between randomly figured syntypes and lectotypes, a problem if type series are not conspecific or (in cases where genders were originally misdiagnosed), not even congeneric. Moreover, the D'ABRERA (1995) volume frequently does not figure types, even if these are present at the BMNH, and relies instead on specimens construed by common usage to represent the same species as the type. This does assure a choice photograph but, without strict reference to types, inclusion of types from other institutions, or resolution of innumerable situations requiring lectotypes or neotypes, workers are again left with only the vagaries of common usage. D'ABRERA (1995) rightly notes that voluminous time would be needed to resolve such problems and these are not a goal of his work (D'ABRERA 1995: vii, 1144). However, his readers should be aware that they "identify" at great risk when certain taxa are not illustrated by the type. For instance, in the speciose "*strephon* group" of "*Thecla*", studies indicated nearly 40% of the taxonomic common usage was at variance with the type material (JOHNSON, AUSTIN, LE CROM & SALAZAR, in press).

Recent studies disciplining identification of species among large sympatric and synchronic series by comparing consistencies of external and internal characters with similar consistencies in type specimens, and which designate lectotype and neotypes, have inevitably led to the recognition of new species (AUSTIN & JOHNSON, 1996 & in press; JOHNSON & AUSTIN ms.; JOHNSON & SOURAKOV, 1993). When consistent sets of characters in series of sympatric and synchronic specimens match those of no extant type (or knowledgeably designated neotype), there is no choice but to describe a new taxon. Otherwise the rules of taxonomic nomenclature (enculcated in the ICZN Code) are meaningless.

### Differing Views of Diversity

Some lepidopterists who want to avoid dealing with "more species", claim "proliferation of names" (to cite one complaint to the present authors, in litt.) leads to an inability to understand connections within the whole. For such workers, more names means more fragmented knowledge, affording less opportunity to recognize relationships. This view is erroneous, however, if the pieces of the puzzle (in this case the "species" of common taxonomic usage) are misidentified in the first place—either by basing common usage on "grades" or making identifications without reference to constellations of characters in type specimens.

There are really two bases underlying views of diversity: (1) purely philosophical constraints concerning the "equation" by which individuals are identified in this or that discipline, and (2) specific methodological questions within particular universes of discourse (like those for systematic biology noted throughout the present discussion). Ontological problems (differences in "how" things are known or recognized) are common to all areas of discourse. In biological systematics, for example, difficulties arise from applying arbitrary LINNAEAN binomial nomenclature to complex biological phenomena. A familiar a priori problem in biology is Paleontology's difficulty in defining species both horizontally ("in one time") and vertically ("through time"). It is an ontological problem precisely concerning how to define "individuals" (in this case species). The matter can be enlightened by examining the identity of "individuals" in contexts wider than systematic biology.

"Individuals" result not only from processes like organic evolution (as in species/individuals of a biota) but also from overt creation (like kinds of automobiles or the "kinds" of "Creation" posited in theistic views of a Creator-God). Organic evolution, manufacturing, and theology constitute very different "universes of discourse" However, the differences between how things are named within these discourses reduces basically to one regarding "equation" (see, for instance, G. T. GHISELIN and D. HULL, both 1992).

LINNAEAN nomenclature is hierarchical and, at its unit level (the "species"), fundamentally binomial. A very different concept is the "Biblical" one (that is, from the Judaic tradition). The Biblical concept is one of "min" or "one name", a fact that can enlighten us regarding fundamental differences between typological and biological views of the origin of diversity. In the Paleontological example of "horizontal" species (species in one time) versus "vertical" species (species through time) the fundamental

gravamen is *time*. It is not by accident that time is pivotal to this ontological problem because it is precisely the role of *time* that distinguishes science from both (1) pre-science and (2) certain religious views.<sup>29</sup>

In science, time is fundamental to process. In pre-science (particularly primitive religion), or even certain modern “creationist” views, time is irrelevant. Evolutionary biology envisions a branching “ascent” from a common ancestor (e.g. “cladogenesis”). This branching “ascent” (as portrayed in character trees or vicariance hypotheses) effects the eventual view of diversity because, coupled with LINNEAN hierarchy, it creates a context in which names multiply as information multiplies. Not only do terminal taxa increase with branching, overall numbers of “individuals” also increase or decrease as problems of paraphyly and polyphyly are resolved.

In typological creationist views like those of D’ABRERA (1995: ix, 1248) “species” are created and then genetically “reduce” over time to “subspecies”, “races”, and “forms” In this view, branching “ascent” (with all its intriguing problems of para- and polyphyly, sister species, sibling species, cryptic species etc.) simply does not exist. It is replaced by could be paraphrased as “descent by reduction” and an entirely different view of diversity results. The broadly construed “species” of this view, based on a few (sometimes only one or two, usually external) characters are very similar to the grades of common usage. Perhaps this is why D’ABRERA (1995: 1248) expresses alliance with certain other taxonomists (e.g. “traditionalists” in his view) but with whom he otherwise differs on the matter of evolution.

A different view of diversity results because typological creationism disregards two fundamental elements of systematic biology: (1) the inherent relationship between methodology and species recognition and (2) the intertwined realities of time and biogeographical phenomena (like allopatric speciation). Claiming that “real” species have nothing to do with positions in an evolutionary hierarchy (D’ABRERA, 1995: ix) is the same as suggesting such species have nothing to do with any biological or biogeographical process (the most obvious being allopatric speciation). If one examines the many interesting examples in SHIELDS’ (1996) discussion of phylogenetic position and species reality, it is apparent that (1) many species are missed if relative phylogenetic position is overlooked (paraphrased simply, “something older may represent a different lineage”) and (2) biogeographic forces themselves are inherent to the processes that establish species as lineages (most basically, the reality of allopatric speciation).

A basis tenant of cladistic systematics and biogeography is that hierarchies of time and space are interrelated. Thus, Roman Catholicism’s “TEILHARDIAN creationism” (which might be best summarized as a “process creationism”) has none of the difficulties with evolutionary process typifying typological creationism.<sup>30</sup> STEPHEN J. GOULD, in a popular and readily accessible discussion of the relationship of evolution and religion (1997), stresses two elements characterizing scientific and religious knowledge—they are *different* universes of discourse and (much because of this, but even generally), they need not be in conflict or contradiction. Indeed, as GOULD notes, such conflicts or contradictions arise only when one or another side in the scientific/religious dialogue is immature.

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29 [Comment by first author]: Essentially, in theology God counts time very differently than humans do.

30 [Comment by first author]: In spite of the new winds blowing in the Catholic Church after Vatican II, the TEILHARDIAN concept (TEILHARD, 1959) is not the official theory of the Church concerning Creation, and will never be. The Church confesses that God created the universe *ex nihilo*, including the Earth with its biota, not in an embryonal state as TEILHARD describes but, rather, having creatures all determinable as plants and animals etc. TEILHARD’S view also ignores Original Sin, which, according to the teaching of the Church, decays not only human beings, but also the whole created world, the biota. Nevertheless, the evolutive concept can be reconciled with the creationist view if we keep in mind that the original meaning of the Latin word “evolutio” is “scrolling out the Torah” This means, with a paradox, that (1) everything has already been created and will later be explained and understood with the help of evolution (scrolling out the corporeal database with the course of time) and (2) nothing is created, but as times go on, more and more knowledge will be available as more and more descendants, species or individuals, are born and pass away. That is the will of the Creator because He does not want *reductio*; His will is *enumeratio* [cf. Genesis 1,23].

In closing, we should note that this entire discussion of science and religion arises only because typological views in systematics (as in typological creationism) are not neutral forces without consequence. Such views exert distinct effects on concepts of diversity and biogeography. This point becomes clear when some effort is made to understand the typological creationist's viewpoint (as in D'ABRERA, 1995: 1248). In short, evolutionists envision branching geneological "ascent"; taxa increase or decrease with ongoing morphological or phylogenetic analysis, etc. In typological creationism, the species is created and *then reduces*, through the processes of time, to various subspecies and forms; species numbers stay stationary or decrease, by extinction. Questions of para- and polyphyly, which would propel most debate concerning monophyly or diversity in modern evolutionary and phylogenetic systematics, do not exist for D'ABRERA because no "ascent" is going on. However, as has been noted concerning all systematic methods which employ "art" (e. g. non-testable hypotheses, see CRAECRAFT, 1974), who will be the arbiter of what, or how many, typological species were created? Such arbiters inevitably revert to the use of one (two, or several, usually external), "key" characters for their typological taxa and so the problem goes round and round.<sup>31</sup>

### Generic Synonymy and NABOKOV's Higher Classification

Concerning higher polyommata taxonomy, it has generally not been noted that NABOKOV's (1945) view of the Neotropical fauna closely followed the taxonomic groundwork on the Palaearctic fauna laid down by STEMPFFER (1937). NABOKOV (1945: 47–48) appears to have made only a single correction to STEMPFFER's generic list, demoting *Lysandra* to synonymy under *Agrodiaetus*. This view was never accepted by Europeans, who traditionally have treated all species or species groups showing any phenological or morphological "gap" as separate genera (see HIGGINS, 1975 and most recently TUZOV, 1993). The problem with such extreme taxonomic splitting has been that, amongst larger samples of polyommata diversity, it is often impossible to decide into which of these myriad genera certain species should be placed. As has been shown in recent revisions of the Neotropical fauna by BÁLINT & JOHNSON (see, particularly, *Pseudolucia* [BÁLINT, 1995b; BÁLINT & JOHNSON, 1995b]) there is more taxonomic utility in maintaining large monophyletic genera. Thus, regarding the many names available in the Old World, one can use lower categorical ranks, like the subgenus, to distinguish subelements of various distinction. Thus all the generic names synonymized here could be used as subgenera, if desired.

The Nearctic genera erected by NABOKOV were controversial and many were not widely accepted, but his Neotropical generic entities stand out by having proved to be natural groups (see BÁLINT & JOHNSON, 1995a). Ironically, one might think that NABOKOV worked at a disadvantage given the sparse material available to him (see BÁLINT & JOHNSON, 1995c, tables 1 and 2). Yet, it is possible that his classification for the Neotropical fauna was successful at the generic level because this fauna had not been touched before and was, therefore, not already encumbered with names. Later, NABOKOV wrote (1973: 320) "I am perfectly willing to demote the whole of my subfamily Plebejinae to a supergenus or genus *Plebejus* but only under the condition that it includes exactly the same species, in the same groupings ("subgenera" or numbered sections, as you will) and in the same sequence of groups without intrusions of groups assigned structurally to other "subfamilies" "

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31 Discussion of D'ABRERA (1995) herein is in no way meant as an "attack" either on D'ABRERA or his work. We agree with many of the positive comments of PIEGLER (1996) concerning D'ABRERA's photofolios and D'ABRERA has been clear concerning both the intentions of, and constraints on, his many pictorial works. We only wish to point out that the methods used by D'ABRERA, and thus transferred to the readers who use his books for identification purposes, are not neutral in either taxonomic or systematic consequence. To the contrary, his methods have distinctive effects concerning views of diversity and biogeography.

As recent revisionary work has shown, at the generic level NABOKOV correctly recognized the monophyly of the Neotropical polyommata genera. He erred only by omission, in not being able to comprehend the larger affinities of these genera with other polyommata (BÁLINT & JOHNSON, 1995a; JOHNSON & BÁLINT, 1995).

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Two new replacement names herein have employed our tradition of using, where appropriate, names derived from VLADIMIR NABOKOV's life or writings. Since 1995 we have been aided in this effort by a committee provided by the Board of Directors of the International VLADIMIR NABOKOV Society and coordinated by Dr. D. BARTON JOHNSON (University of California, Santa Barbara, USA), a past editor of NABOKOV Studies. New "NABOKOVian" names designated herein derive from the suggestions of this committee; the etymologies of the names explain their meaning and also note the committee person responsible for their choosing, in the present case NABOKOV scholars Dr. ELLENDEA PROFFER and Dr. SIMON KARLINSKY.

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## Appendix

(Description of six polyommatine lycaenid species by ZSOLT BÁLINT)

### 1. *Agríades kurtjohnsoni* BÁLINT, **spec. nov.** (colour Plates 3–4, figs. 4–5)

#### Diagnosis

Wings. Male dorsal wing ground colour dusky lavender blue with wide black margin; discoidal spot very small, almost invisible; ventral hindwing colour greenish with typical polyommatine pattern, markings white, reduced with vestigial pupilation. Female dorsal wing colour brown with blue basal suffusion; discoidal spot large and blue. Morphology. Male genitalia commonplace *Agríades* with "humped" valva (see FERNANDEZ-RUBIO, 1976, pls. 48–51). Female terminalia plain, with lateral, pointed extension on both sides.

#### Description

Male. Dorsal wing ground colour unicolourous lavender blue with darkly coloured veins, black marginal border wide, discoidal line indistinct, fringes white, all vein terminalia black; ventral forewing grey in postmedian and marginal area, basal region suffused with greenish scales, discoidal and postdiscal spots scarcely visible, submarginal pattern also indistinct; ventral hindwing ground colour greenish with large basal and postmedian spots, marginal area grey with suffused pattern; forewing length: 12 mm (holotype), 10–11 mm (paratypes). Female. Dorsal wing ground brown with blue basal suffusion and blue discoidal spot on forewing; ventral pattern similar to male; forewing length: 13 mm (allotype), 12 mm (paratype).

Male genitalia. General appearance as in all *Agríades*. Uncus horseshoe shaped, gnathos weak and upturned, juxtal arms long, slender and divergent, valval rostellum strong with heavily dentated terminus.

Female genitalia. Ductus bursae evertable, short and membranous, terminus plain with pointed lateral extension on both sides.

#### Additional descriptive notes

The new species can be easily separated from the sister taxa *morsheadi-janigena* by the following external characters: 1. ventral hindwing ground greenish (brownish in *morsheadi-janigena*); 2. the hindwing ventral lunules are smaller and distinct (very large and coealescent in *morsheadi-janigena*) and 3. female dorsal forewing with blue discoidal spot (brown in *morsheadi-janigena*).

#### Types

Holotype ♂: "Nepal, Jargeng Khola, 14.000 ft, 4.VII.1950; B.M. Exp. to Nepal, M.M. 1950–649; gen. prep. No. 523, BÁLINT"

Allotype ♀: "Nepal, Sabze Khola, 13.800 ft., 19.VII. 1950; B.M. Exp. to Nepal, M.M. 1950–649; gen. prep. No. 526, BÁLINT"

Paratypes: 1 ♂ (Nepal: Khangsar, 15000 ft, 27.VII.1950), 1 ♂ (Nepal: Khangsar, 16000 ft, 29.VII. 1950), 1 ♂ (Nepal: Jargeng Khola, 14000 ft, 6.VII.1950), 1 ♂, 1 ♀ (Nepal: Sabze Khola, 12500 ft, 20.VII.1950). All deposited in BMNH excluding Khangsar paratype, which is in HHNM.

#### Bionomics

The type specimens were collected exclusively in July, at very high altitudes. Larval host is unknown.

#### Etymology

"*kurtjohnsoni*" is an adjective in apposition, in honour of lepidopterist Dr. KURT JOHNSON, working at the American Museum Natural History (New York) with whom the senior author of the present paper has co-authored numerous publications on Neotropical lycaenids.

2. *Albulina gaborronkayi* BÁLINT, **spec. nov.**  
(colour plates 3–4, fig. 7)

Diagnosis

Wings. Male dorsal wing ground colour entirely brown with scattered gleaming bluish green scales; discoidal spot very small, almost invisible; ventral hindwing colour greyish with strongly reduced polyommata pattern and extended gleaming greenish blue basal suffusion. Morphology. Male genitalia commonplace *Albulina* (BÁLINT, 1991: figs 136–142) but with slender valva.

Description

Wings. Male. Dorsal wing ground colour unicolourous brown with scattered bluish green scales, discoidal line indistinct, fringes basally brownish, apically white; ventral forewing unicolourous grey, discoidal and postdiscal spots well visible, submarginal pattern indistinct; ventral hindwing basal and median area gleaming bluish green, marginal area grey with reduced pattern; forewing length: 10.5 mm (holotype), 11 mm (paratype). Female. Unknown.

Male genitalia. General appearance as in all *Agriades*. Uncus slender, gnathos weak and upturned, juxtal arms medium sized, slender and more or less parallel, aedeagus wide and short with conspicuously short suprazonal element, valval rostellum strong with hooked terminus.

Additional descriptive notes

The new species can be easily separated from the sister taxa *felicitis-youngusbandi* by the following external characters: 1. smaller than *felicitis-youngusbandi* (these two taxa are considerably larger); 2. hindwing dorsal submarginal orange lunules completely missing (large and coalescent in *felicitis*, somewhat reduced but visible in *youngusbandi*); 3. hindwing ventral gleaming suffusion reduced (extended in *felicitis-youngusbandi*).

Types

Holotype ♂: "S. E. Thibet: Ralung, 26.VIII.1924, W. H. EVANS; gen. prep. No. 702, BÁLINT"

Paratype ♂: "Everest Ex., Raphu, 15.000 ft., 31.VII., '21; W. H. EVANS, B.M.1932–274; gen. prep. No. 703, BÁLINT"

All deposited in BMNH.

Bionomics

The type specimens were collected at very high altitudes. Larval host is unknown.

Etymology

The name "*gaborronkayi*" is an adjective in apposition, in honour of lepidopterist Mr. GABOR RONKAY (Budapest), specialist on the noctuid subfamily Cucullinae, childhood friend of the senior author (BÁLINT, 1996) of the present paper.

3. *Polyommatus frauartiana* BÁLINT, **spec. nov.**  
(colour plates 3–4, fig. 8)

Diagnosis

Wings. Male and female dorsal wing ground colour entirely brown with scattered gleaming greenish scales; discoidal spot small, almost invisible; ventral hindwing colour greyish brown with commonplace polyommata pattern, with gleaming greenish basal suffusion and white horizontal median streak. Morphology. Male and female genitalia commonplace *Agrodiaetus* (cf. NEKRUTENKO, 1985: fig. 123, and KOLEV & DE PRINS, 1995: figs 1–6).

Description

Male. Dorsal wing ground colour unicolourous brown with scattered gleaming greenish scales, discoidal line indistinct, fringes basally entirely white; ventral forewing unicolourous brownish grey with large postdiscal spots and salient submarginal markings; ventral hindwing with well developed polyommata pattern and conspicuous horizontal median streak from base to margin, basal and median area gleaming bluish green, submarginal area grey with large reddish brown, white and orange spots; forewing length: 14 mm (holotype and paratype). Female. Similar to male, forewing length: 13 mm (paratype).

Male genitalia. General appearance as *Polyommatus*. Uncus wide and horseshoe shaped, gnathos weak, short and upturned, juxtal arms very long, slender and divergent, aedeagus long and narrow with conspicuously short suprazonal element; valva very long and slender, rostellum strong, slightly dentated. Female genitalia not studied.

Additional descriptive notes

The new species can be easily separated from the sister taxon *glaucias* by the following external characters: 1. smaller than *glaucias*; 2. male wing dorsum only with scattered gleaming scales (*glaucias* generally suffused with gleaming scales along veins); 3. hindwing ventral median streak complete from base to margin (generally interrupted in *glaucias*).

Types

Holotype "♂: 30.VII.1963., Afghan centr., Band-i-Amir, 3000 m, KASY & VARTIAN; gen. prep. no. 127, BÁLINT"

Paratype ♀ with same locality data. Paratype ♂: "29.VII.1963., Afghan centr., O v Band-i-Amir, 3600 m, KASY & VARTIAN leg."

All deposited in VARTIAN Collection, Naturhistorisches Museum (Vienna, Austria).

Bionomics

The type specimens were collected exclusively in July, at relatively high altitudes. The biotope is characterized by KASY (1965: 664). Larval host is unknown.

Etymology

The name "*frauartiana*" is an adjective in apposition, in honour of lepidopterist Mrs EVA VARTIAN (Vienna, Austria), who presented her valuable Lepidoptera collection very recently to the Naturhistorisches Museum, Vienna (LÖDL, 1996).

4. *Polyommatus fabiani* BÁLINT, **spec. nov.**  
(colour plates 3–4, fig. 9, left)

Diagnosis

Wings. Male forewing short and wide, with pointed apex; dorsal wing ground colour luminous blue with relatively wide black marginal border; ventral hindwing ground colour light brownish grey with commonplace, but strongly reduced, polyommataine pattern with gleaming greenish basal suffusion and white horizontal median streak. Morphology. Male genitalia commonplace *Agrodiaetus* (cf. NEKRUTENKO, 1985: fig. 123). Female unknown.

Description

Male. Dorsal wing ground colour unicolourous luminous blue with black veins and relatively wide black border, but apex blue, discoidal line indistinct, fringes basally greyish; ventral forewing costal area very light unicolourous brownish grey, anal area darker, discoidal and postdiscal spots large, submarginal markings salient; dorsal hindwing with antemarginal spots in each cell; ventral hindwing with reduced polyommataine pattern and conspicuous horizontal median streak from base to margin, basal and median area gleaming bluish green, median area warm brownish grey with indistinct spots; submarginal area with salient polyommataine pattern. Forewing length: 15 mm (holotype and paratype).

Male genitalia. General appearance as *Polyommatus (Agrodiaetus)*. Uncus wide and horseshoe shaped, gnathos weak, short and upturned, juxtal arms very long, slender and divergent, aedeagus long and narrow with conspicuously short suprazonal element; valva very long and slender, rostellum strong, slightly dentated.

Additional descriptive notes

The new species can be easily separated from the other three blue Mongolian "*Agrodiaetus*" species (*damon*, *damone* and *walteri*)<sup>32</sup> by the following external characters: 1. forewing costa short with pointed apex (longer and not so pointed in *damon*, *damone* and *walteri*); 2. forewing marginal border not so wide (more extended in *damon* and *walteri*, very narrow in *damone*) and 3. dorsal wing ground colour deeper blue without greenish shade (light blue in *damone*, greenish in *damon* and *walteri*).

Types

Holotype ♂: "Mongolia, Dundgovi aimak, 4 km NE of Mandalgovi, 106°20'E 45°48'N; 20.VII.1986, exp. Gy. FÁBIÁN, M. HREBLAY, L. PEREGOVIĆ, G. RONKAY; gen. prep. no. 709, BÁLINT." Paratype, male, with same locality data. Both deposited in HHNM.

Bionomics

The type specimens were collected exclusively in July, on an *Artemisia* steppe on sand. The biotope is briefly characterized in BÁLINT (1989a: 94, fig. 21). Larval host is unknown.

Etymology

The name "*fabiani*" is an adjective in apposition, in honour of lepidopterist Mr. GYÖRGY FÁBIÁN (Budapest, Hungary), who participated the expedition organized by Hungarian lepidopterists, which collected the type specimens (BÁLINT, 1989a).

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<sup>32</sup> *Polyommatus damone walteri* DANTSCHENKO & LUKHTANOV, 1993 (TL: NW Mongolia) (cf. colour plates 3–4, fig. 9, right) is certainly not a *damone* subspecies because *P. damone altaica* (ELWES) and *walteri* are sympatric in the district of Great Lakes, NW Mongolia (cf. BÁLINT, 1988: 100 and 1989b: 108).

5. *Polyommatus delessei* BÁLINT, **spec. nov.**  
(colour plates 3–4, fig. 10)

Diagnosis

Female. Forewing short and wide, with rounded apex; dorsal wing ground colour warm brown; fringes grey with yellow shade; ventral ground colour greyish brown, forewing discoidal and postdiscal spots larger than on hindwing, submarginal area patterned. Morphology of genders unknown. Chromosome number:  $n = 42-47$ .

Description

Male. Unknown. Female. Dorsal wing ground colour unicolorous brown with a weak bronze shade in distal area, discoidal line invisible; fringes yellowish grey; ventral forewing ground colour greyish brown, discoidal line and postdiscal spots large, submarginal markings visible as large brown and little light grey intercellular spots; ventral hindwing ground colour as on forewing but with very narrow discoidal line and smaller postdiscal spots, submarginal pattern reduced but complemented with pale brown antimarginal patch in each cell. Forewing length: 11 mm (holotype), 10 and 12 mm (paratypes). Female genitalia unknown.

Additional descriptive notes

The new species can be separated from the two sympatric Iranian "*Agrodiaetus*" taxa (*baltazardi* and *kermansis*) by the following characters: 1. smaller (the mentioned taxa are larger); 2. forewing shape wider and apex rounded (not so wide and pointed in *baltazardi* and pointed in *kermansis*); 3. dorsal forewing postdiscal spots very large comparing with hindwing markings (smaller in the mentioned taxa). DE LESSE removed the abdomens of the type specimens in the process of determining the chromosome number (DE LESSE 1962: 311). I could not locate dissections for the specimens at the MNHN (see below). Perhaps the abdomens were consumed by chromosome analysis; however, DE LESSE stated he established the chromosome number on the basis of a single specimen.

Types

Holotype: "Kuh-i-Laihzar (Kerman), Iran SE 2800–3600 m, 26–28-VIII-1961, H. DE LESSE". deposited in MNHN. Paratypes, two females, with same data as holotype, deposited in MNHN and HHNM.

Bionomics

The type specimens were collected at the end of July, at relatively high elevation (2800–3000 m) on an "*Artemisia* steppe" rich in Leguminosae (DE LESSE, 1962: 307–308).

Etymology

The name "*delessei*" is an adjective in apposition, in honour the late Hubert DE LESSE, who thoroughly studied the *Agrodiaetus* s. l. taxa of the Palearctic region. He collected the type series and noted the uniqueness of these specimens (DE LESSE, 1962: 311).

6. *Madeleinea gradoslamsi* BÁLINT, **spec. nov.**  
(colour plates 3–4, fig. 11)

Diagnosis

Wings. Male forewing shape short and wide with pointed apex, dorsal wing ground colour tinted blue; ventral hindwing with postmedian spots, median band continuous from base to anal margin. Female similar to male, but with wider wingshape and silvery blue dorsal ground colour. Morphology. Resembles *M. pacis* and *M. sigal* but with more humped male genital valva and female genitalia with minute sclerotized henia.

Description

Male. Dorsal wing ground colour tinted blue, veins black, discoidal line not visible, black border equally wide along margin; ventral forewing ground brown, discoidal and postdiscal spots relatively large with pale halos, veins darker, well visible; submarginal area not marked; ventral hindwing with commonplace *Madeleinea* pattern (see BÁLINT & JOHNSON, 1995c) with extended silvery elements, coalescent median band and conspicuous pseudovitta. Forewing length: 9 mm (paratype). Female. Similar to male, but with silvery blue dorsal wing ground colour. Forewing length: 9 mm (holotype). Male genitalia. General appearance of *Madeleinea*. Uncus long and pointed, gnathos weak, short and upturned, juxtal arms very long, slender and divergent, aedeagus long and narrow with conspicuously long and basally sclerotized suprazonal element; valva very long but humped with high BAIRD's angulation, rostellum strong. Female genitalia. General appearance of *Madeleinea*. Henia strongly sclerotized with slightly convex distal edges and very minute comparing anterior lamella (anterior lamella width three times that of length).

Additional descriptive notes

The new species can be easily separated externally from the similar Peruvian *Madeleinea* species (*M. sigal*, *M. pacis* and *M. cobaltana*) by the following external characters: 1. much smaller than the mentioned taxa; 2. ventral hindwing with relatively narrow but continuous median band (continuous but much wider in *pacis*, interrupted in *sigal* and *cobaltana*). *M. ardisensis* BÁLINT & LAMAS, 1996 is also small, but with more complex ventral hindwing pattern (median band interrupted, silvery elements scattered and but more extended).

Types

Holotype ♀: "Peru, Ayacucho, 1447/7400, 34 km SE Puquio, 3750 m, 1995.II.16., leg. BÁLINT, GRADOS & LAMAS; gen. prep. no. 568, BÁLINT", deposited in MUSM.

Paratype ♂, with same locality data as holotype, deposited in HNHM.

Bionomics

The type specimens were collected exclusively in July, in high Andean puna with sparse vegetation along a brook, at high elevation (BÁLINT, 1997). Larval host is unknown.

Etymology

The name "*gradoslamsi*" is an adjective in apposition, in honour of lepidopterists Mr. JUAN GRADOS (Chosica, Peru) and Dr. GERARDO LAMAS (Lima, Peru), who were collecting together with the author in the Andes (BÁLINT, 1997).

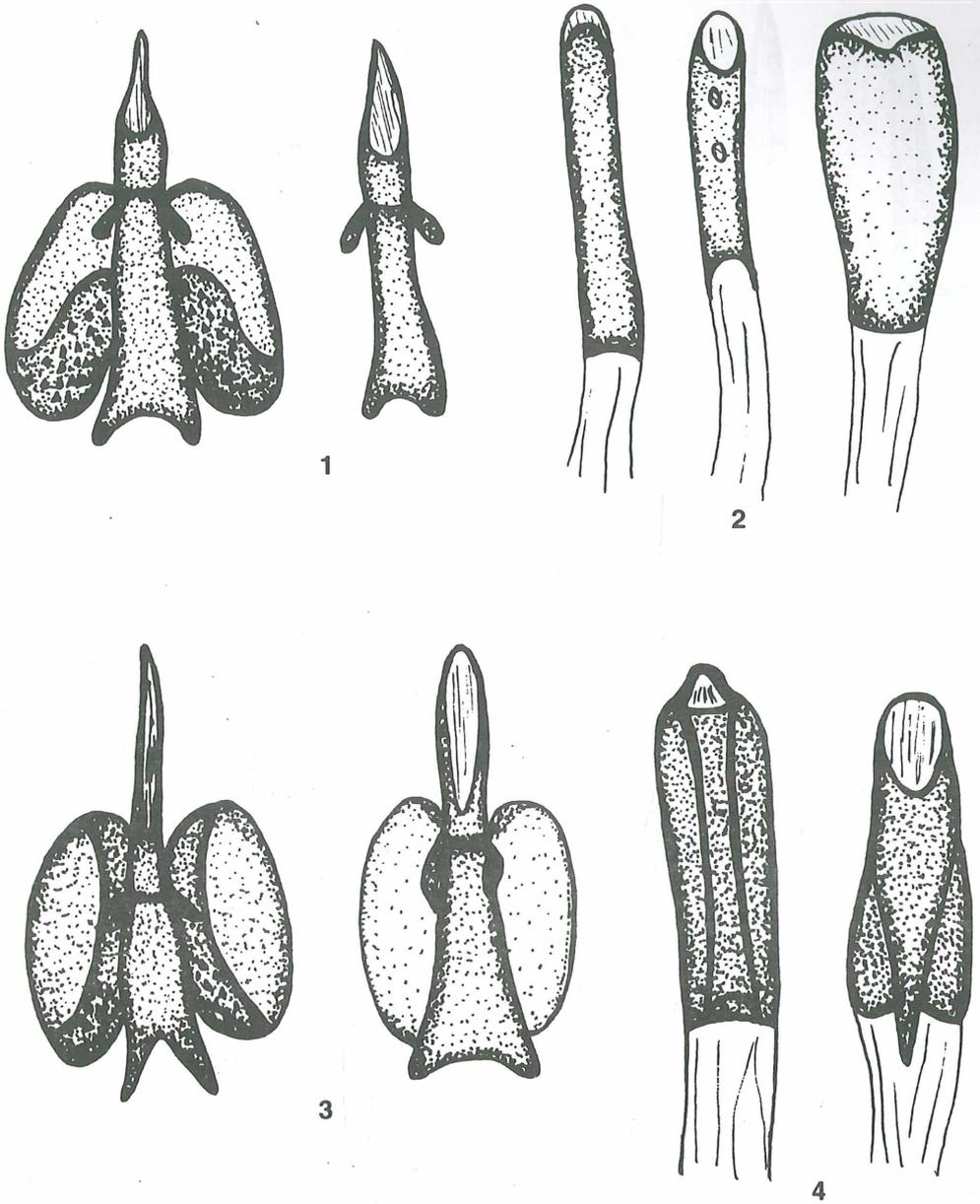


Fig. 1: Male genital aedeagus of certain NABOKOVIA GENUS-group taxa. Left: *Echinargus martha* (DOGNIN); right: *Nabokovia cuzquenha* (BÁLINT & LAMAS). Fig. 2: Female genital terminalia of certain NABOKOVIA GENUS-group taxa. Left: *Echinargus isola* (REAKIRT); middle: *Nabokovia cuzquenha* (BÁLINT & LAMAS); right: *Echinargus martha* (DOGNIN). Fig. 3: Male genital aedeagus of certain *Pseudolucia* taxa. Left: *Ps. lanin* BÁLINT & JOHNSON; right: *Ps. plumbea* (BUTLER). Fig. 4: Female genital terminalia of certain *Pseudolucia* taxa. Left: *Ps. lanin* BÁLINT & JOHNSON; right: *Ps. plumbea* (BUTLER).

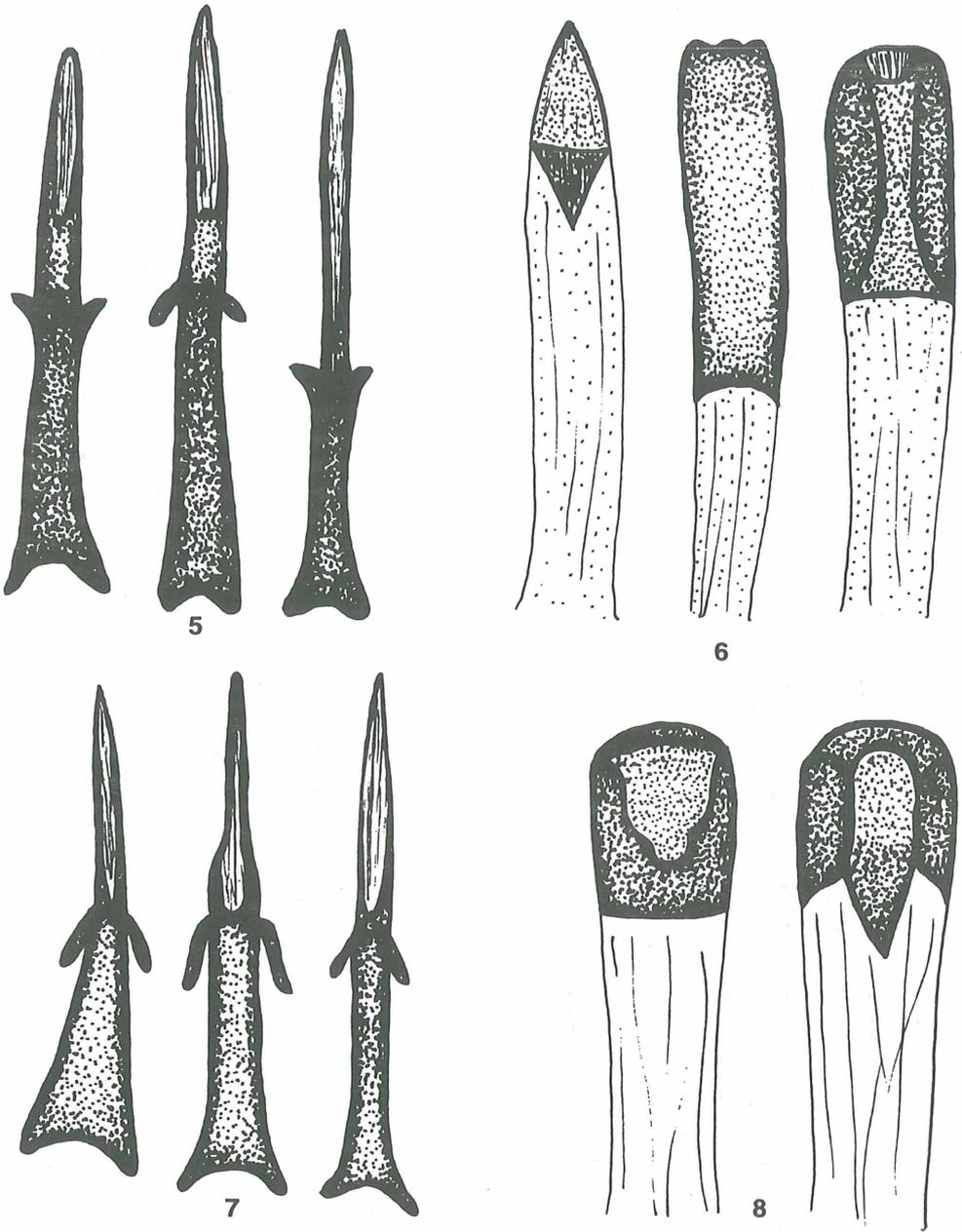


Fig. 5: Male genital aedeagus of certain *Aricia* taxa. Left: *A. cramera* (ESCHSCHOLTZ); middle: *A. saepiolus* (BOISDUVAL); right: *A. myrmecias* (CHRISTOPH). Fig. 6: Female genital terminalia of certain *Aricia* taxa. Left: *A. cramera* (ESCHSCHOLTZ); middle: *A. saepiolus* (BOISDUVAL); right: *A. icarioides* (BOISDUVAL). Fig. 7: Male genital aedeagus of certain *Madeleinea* taxa. Left: *M. nodo* BÁLINT & JOHNSON; middle: *M. pacis* (DRAUDT); right: *M. moza* (STAUDINGER). Fig. 8: Female genital terminalia of certain *Madeleinea* taxa. Left: *M. moza* (STAUDINGER); right: *M. huascarana* (BÁLINT & LAMAS).

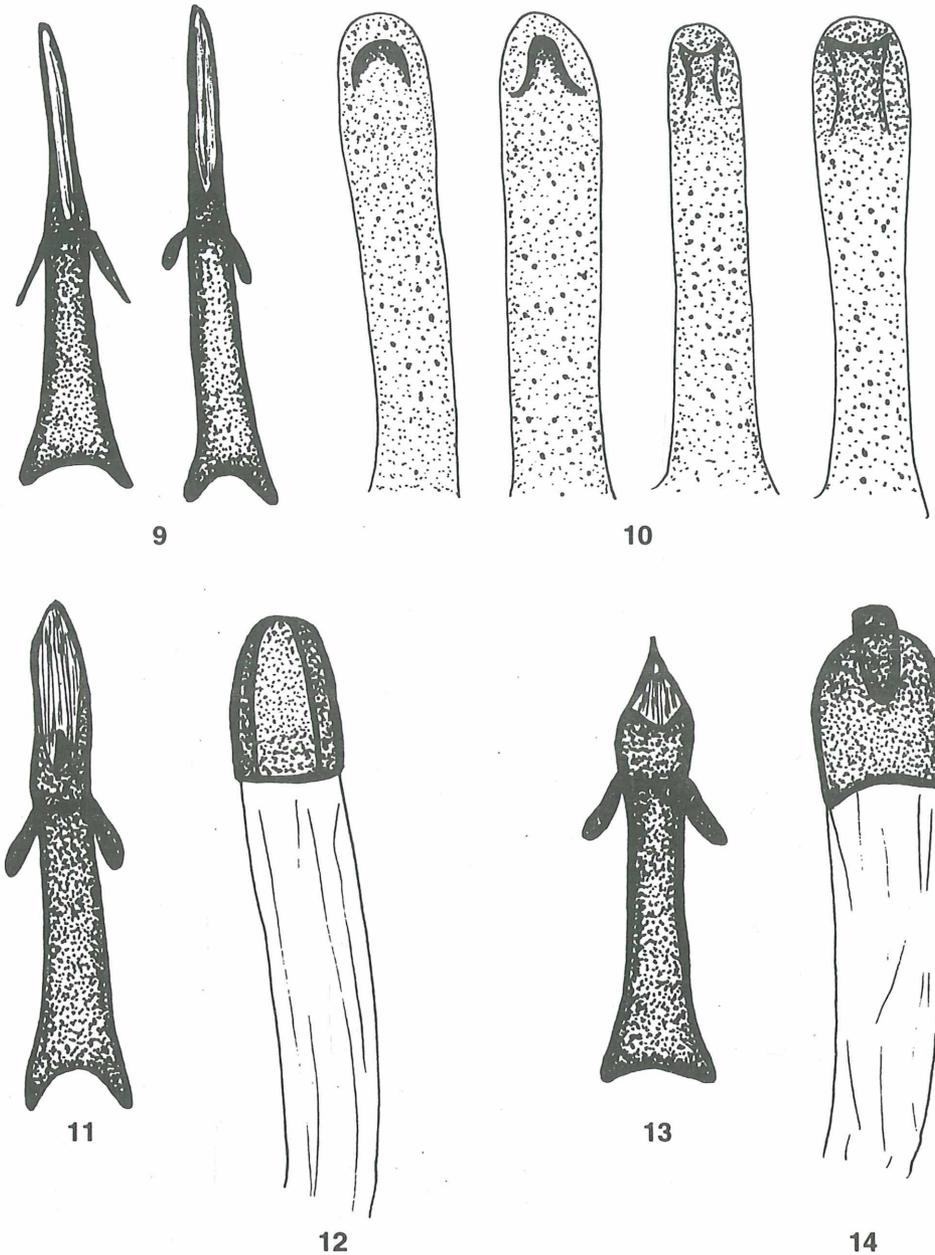
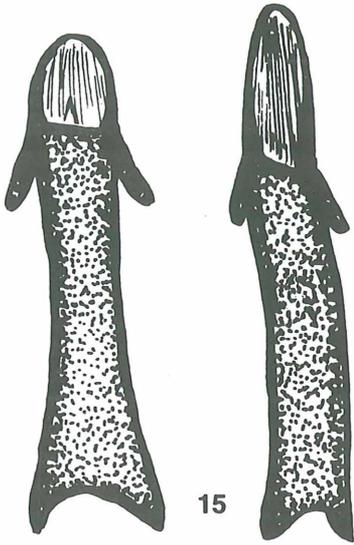
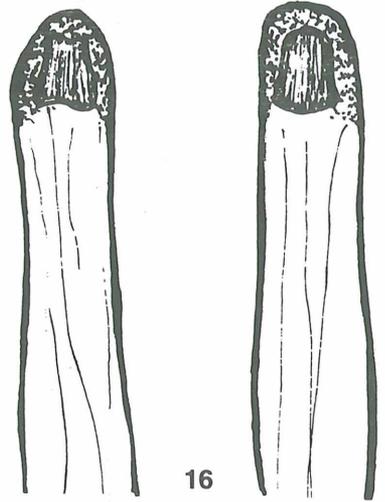


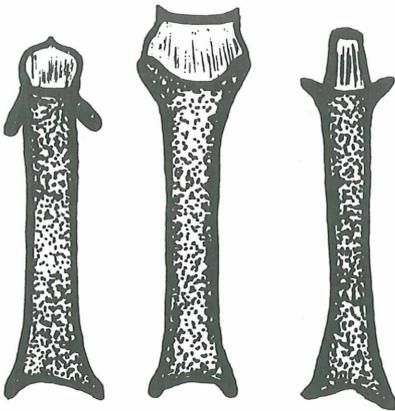
Fig. 9: Male genital aedeagus of certain *Plebejus* taxa. Left: *P. idas* (LINNAEUS); right: *P. lucifera* (STAUDINGER). Fig. 10: Female genital terminalia of certain *Plebejus* taxa. Left: *P. idas* (LINNAEUS); middle, left: *P. corsicus* (BELLIER); middle, right: *P. ardis* BÁLINT & JOHNSON; right: *P. subsolanus* (BREMER). Fig. 11: Male genital aedeagus of *Chilades cleotas* (GUÉRIN-MÉNEVILLE). Fig. 12: Female genital terminalia of *Chilades cleotas* (GUÉRIN-MÉNEVILLE). Fig. 13: Male genital aedeagus of *Paralycaeides shade* BÁLINT. Fig. 14: Female genital terminalia of *Paralycaeides shade* BÁLINT.



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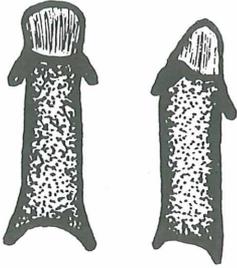


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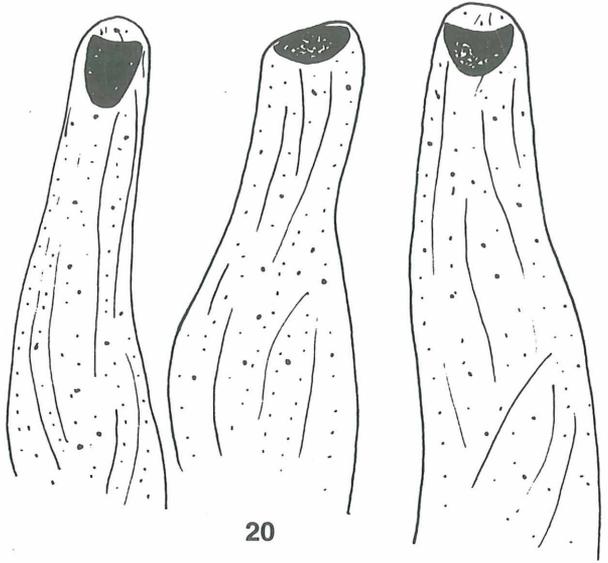


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Fig. 15: Male genital aedeagus of certain *Agriades* taxa. Left: *A. aquilo* (BOISDUVAL). Right: *A. arcaseia* (FRUHSTORFER). Fig. 16: Female genital terminalia of certain *Agriades* taxa. Left: *A. pyrenaicus* (BOISDUVAL); Right: *A. wosnesenskii* (MÉNÉTRIÈS). Fig. 17: Male genital aedeagus of certain *Polyommatus* taxa. Left: *P. dorylas* (DENIS & SCHIFFERMÜLLER); middle: *P. icarius* (ESPER); right: *P. turanica* (HEYNE). Fig. 18: Female genital terminalia of certain *Polyommatus* taxa. Left: *P. dorylas dorylas* (DENIS & SCHIFFERMÜLLER); middle: *P. icarius* (ESPER); right: *P. turanica* (HEYNE).

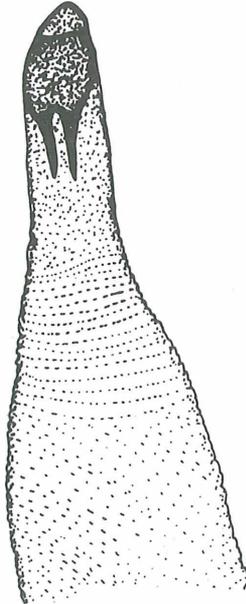


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Fig. 19: Male genital aedeagus of certain *Albulina* taxa. Left: *A. luanus* (EVANS); right: *A. loewi* (ZELLER). Fig. 20: Female genital terminalia of certain *Albulina* taxa: Left: *A. morgiana* (KIRBY); middle: *A. alcedo* (CHRISTOPH); right: *A. omphisa* (MOORE).



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Fig. 21: Female genital terminalia of *Eicochrysops nandius* (BETHUNE-BAKER, 1906).

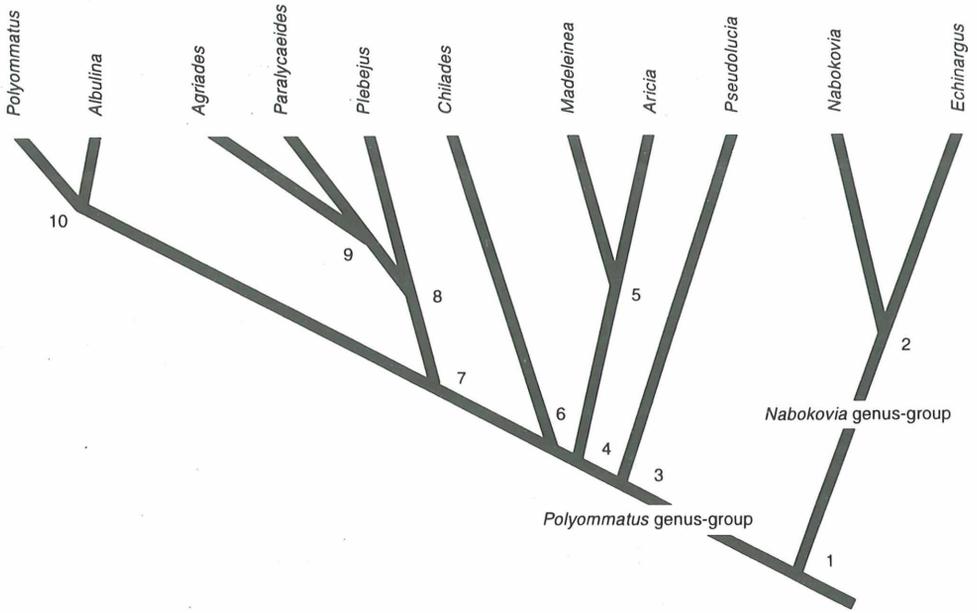


Fig 22: Hypothetical Branching Diagram of the *Polyommatus*-group and outgroups

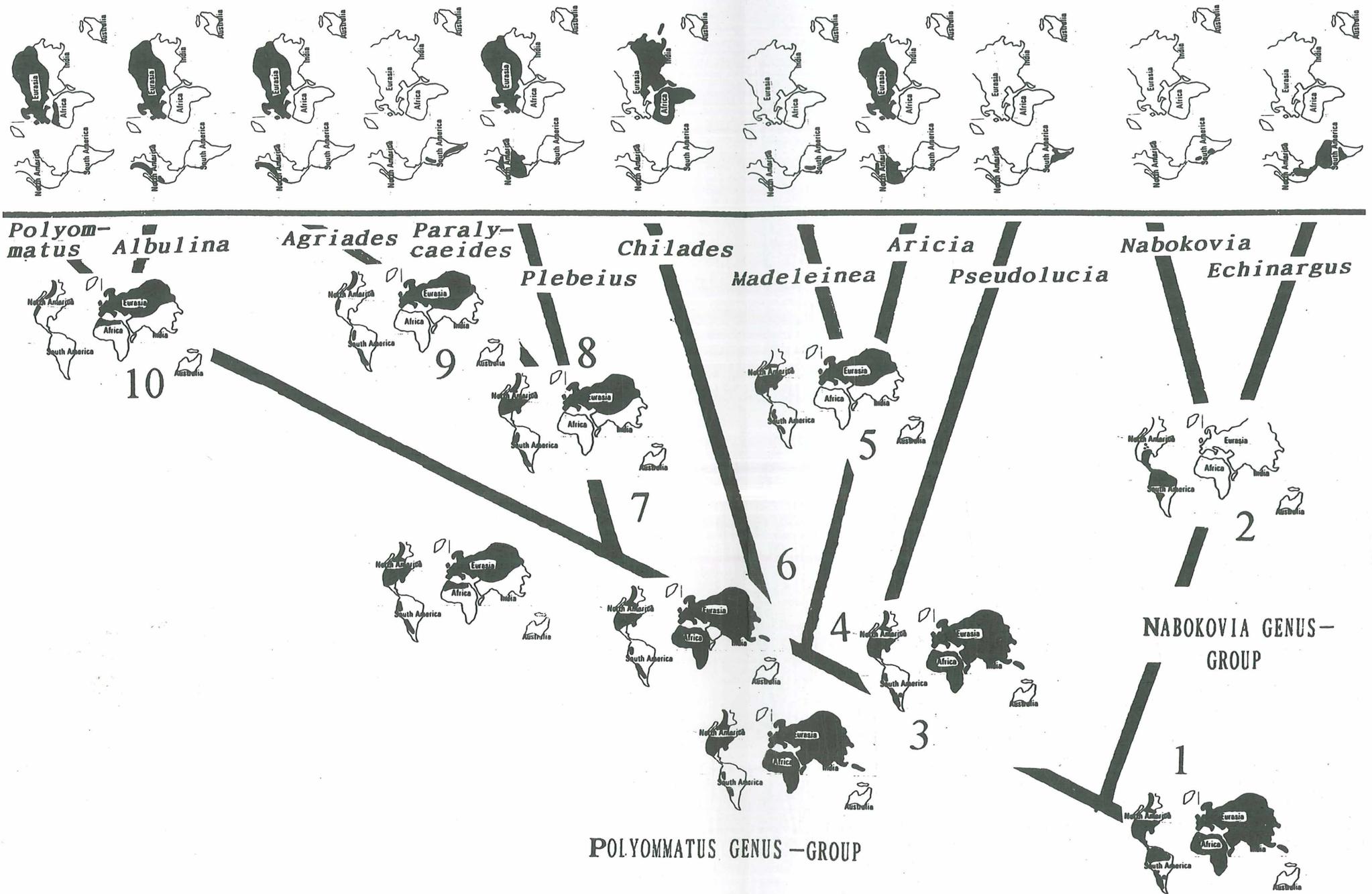


Fig. 23: Area Diagram of the *Polyommatus* Section and outgroups. Each node and terminal taxon is accompanied by a generalized distribution for the clade represented by that node or terminal taxon.

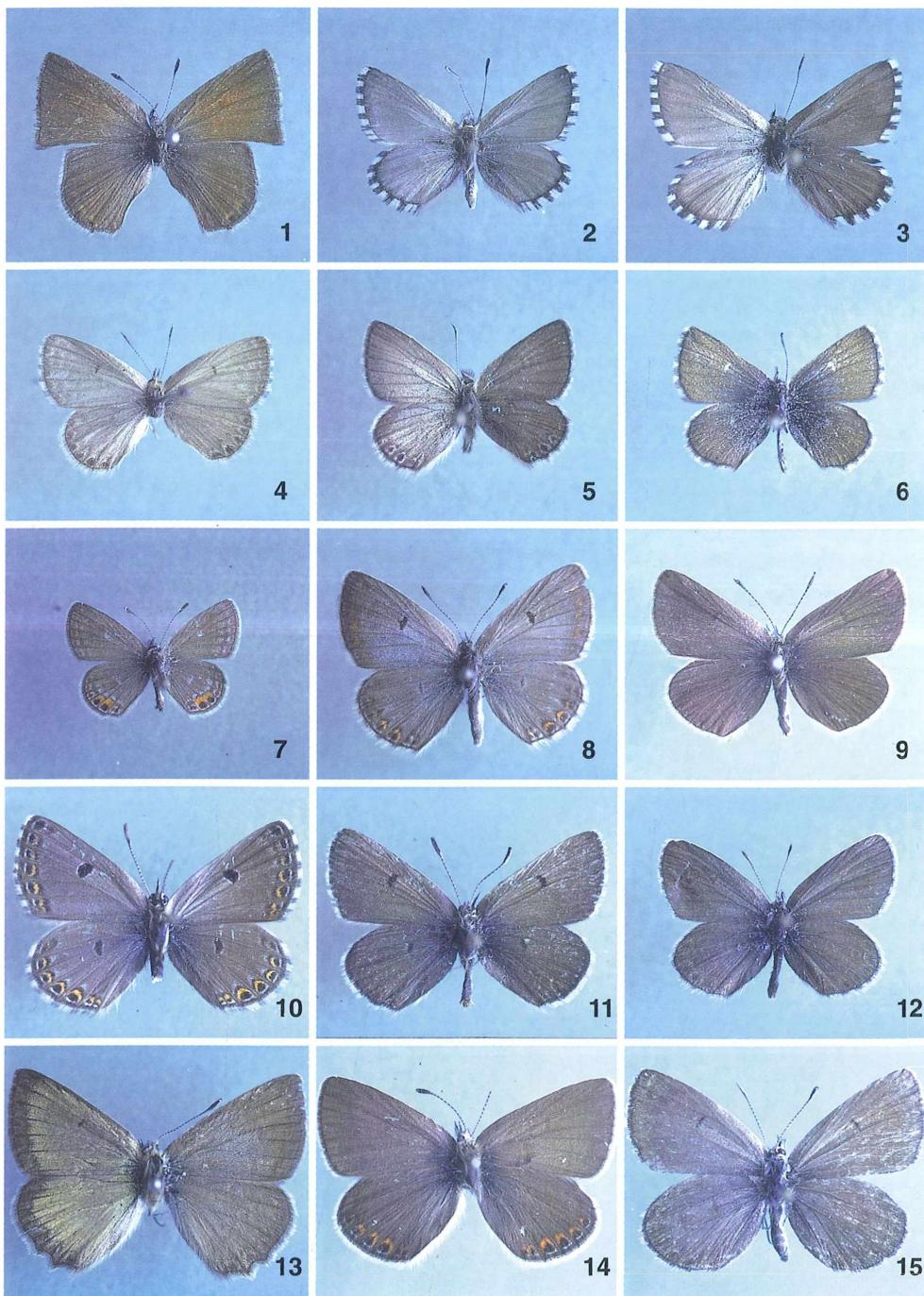


Color plates 1 - 4

Color plate 1: Wing uppersides of discoloured polyommata lycaenid taxa

- Fig. 1: *Nabokovia cuzquenha*, ♂, paratype (HNHM)  
Fig. 2: *Pseudolucia avishai*, ♂, holotype (HNHM)  
Fig. 3: *Ps. nequeniensis*, ♂, paratype (HNHM)  
Fig. 4: *Ps. parana*, ♂, Castro, Parana (BMNH)  
Fig. 5: *Madeleinea moza*, ♂, Argentina, Prov. Jujuy, Cerro Amarillo (HNHM)  
Fig. 6: *Paralycaeides inconspicua*, ♂, Peru, Garela NP (HNHM)  
Fig. 7: *Chilades trochylus*, ♂, Asia minor, Ak Cheir (HNHM)  
Fig. 8: *Aricia vandarbani*, ♂, Persia, Elburs Mts., Tacht i Suleiman (HNHM)  
Fig. 9: *Aricia persephatta*, ♂, Kuldja (HNHM)  
Fig. 10: *Plebejus vogelii*, ♂, Marokko, High Atlas, Taghzeft Pass (HNHM)  
Fig. 11: *Plebejus rutilans*, ♂, Afghanistan, Hindukush, Salang Pass (HNHM)  
Fig. 12: *Plebejus ida*, ♂, Mongolia, Yulin Am (HNHM)  
Fig. 13: *Polyommatus marcidus*, ♂, Persia, Elburs Mts., Tacht i Suleiman (HNHM)  
Fig. 14: *Albulina felicis*, ♂, Wassekou, Szetchwan-China (HNHM)  
Fig. 15: *Aricia astorica*, ♂, Baltistan, Skardu (HNHM)

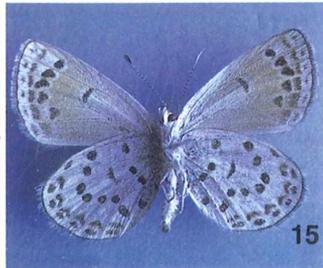
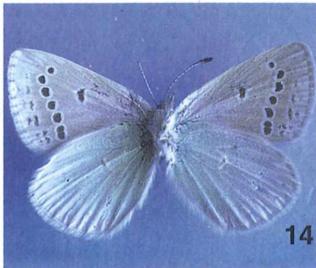
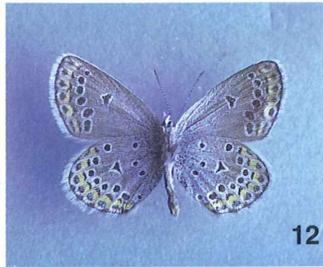
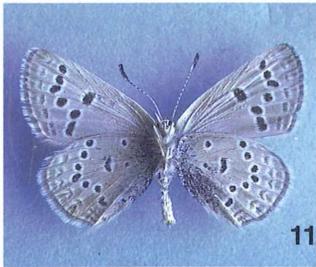
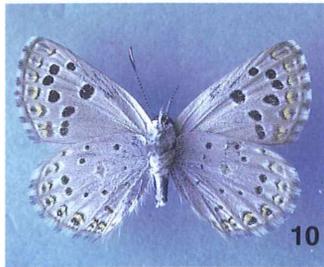
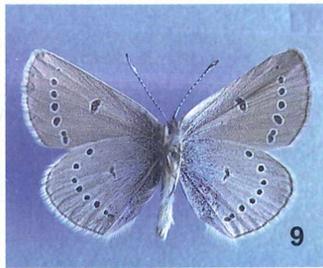
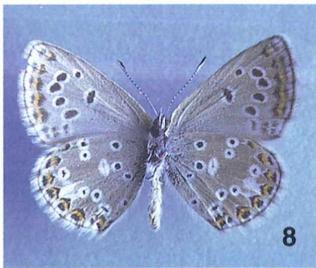
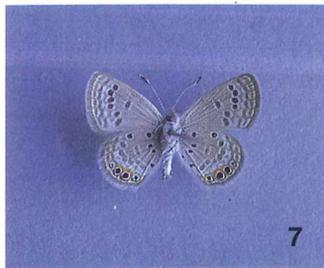
Colour plate 1



Color plate 2: wing undersides, as colour plate 1.

- Fig. 1: *Nabokovia cuzquenha*, ♂, paratype (HNHM)  
Fig. 2: *Pseudolucia avishai*, ♂, holotype (HNHM)  
Fig. 3: *Ps. nequeniensis*, ♂, paratype (HNHM)  
Fig. 4: *Ps. parana*, ♂, Castro, Parana (BMNH)  
Fig. 5: *Madeleinea moza*, ♂, Argentina, Prov. Jujuy, Cerro Amarillo (HNHM)  
Fig. 6: *Paralycaeides inconspicua*, ♂, Peru, Garela NP (HNHM)  
Fig. 7: *Chilades trochylus*, ♂, Asia minor, Ak Cheir (HNHM)  
Fig. 8: *Aricia vandarbani*, ♂, Perisa, Elburs Mts., Tacht i Suleiman (HNHM)  
Fig. 9: *Aricia persephatta*, ♂, Kuldja (HNHM)  
Fig. 10: *Plebejus vogelii*, ♂, Marokko, High Atlas, Taghzeft Pass (HNHM)  
Fig. 11: *Plebejus rutilans*, ♂, Afghanistan, Hindukush, Salang Pass (HNHM)  
Fig. 12: *Plebejus ida*, ♂, Mongolia, Yulin Am (HNHM)  
Fig. 13: *Polyommatus marcidus*, ♂, Persia, Elburs Mts., Tacht i Suleiman (HNHM)  
Fig. 14: *Albulina felicis*, ♂, Wassekou, Szetchwan-China (HNHM)  
Fig. 15: *Aricia astorica*, ♂, Baltistan, Skardu (HNHM)

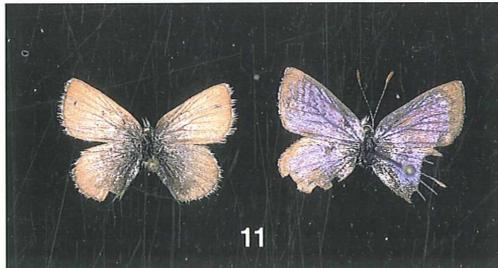
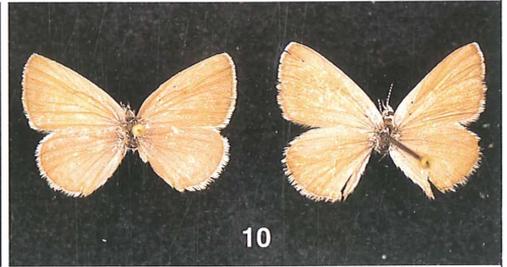
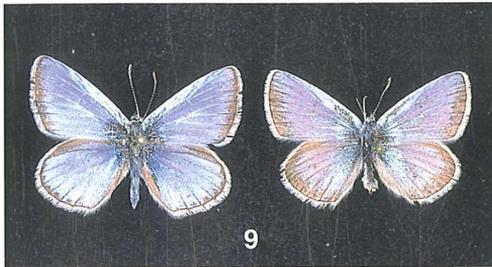
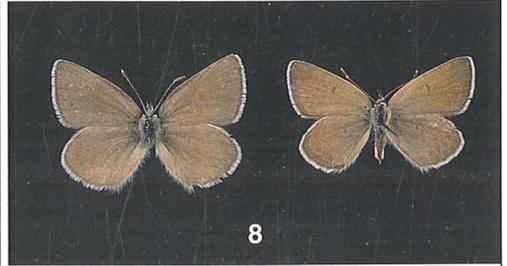
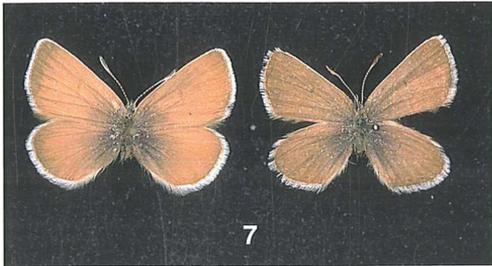
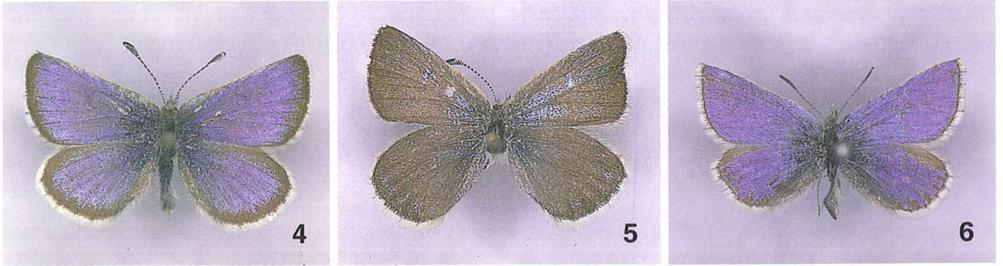
Colour plate 2



Color plate 3: Wing uppersides of certain polyommatae lycaenid taxa.

- Fig. 1: *Polyommatus iranicus*, ♂, Turkey, Prov. Agri, Tahir Gecidi (HNHM)  
Fig. 2: *Polyommatus "ripartii"*, ♂, Uzbekistan, vic. Tashkent, 2500 m (HNHM)  
Fig. 3: *Aricia annulata*, ♂, holotype (BMNH)  
Fig. 4: *Agriades kurtjohnsoni*, holotype (BMNH)  
Fig. 5: *Agriades kurtjohnsoni*, paratype, ♀ (HNHM)  
Fig. 6: *Agriades sikkima*, syntype (BMNH)  
Fig. 7: *Albulina gaborronkayi*, holotype (BMNH) (left), paratype (BMNH) (right)  
Fig. 8: *Polyommatus frauvariana*, holotype (left) and paratype ♀ (right) (NMW)  
Fig. 9: *Polyommatus fabiani*, holotype (HNHM) (left), *P. wagneri*, ♂, Hasagt Hayhran, Gov'Altay, Mongolia (HNHM)  
Fig. 10: *Polyommatus delessei*, holotype (MNHN) (left), paratype (HNHM) (right)  
Fig. 11: *Madeleinea gradoslamsi*, paratype (HNHM) (left) and holotype (MUSM) (right)

Colour plate 3



Color plate 4: wing undersides, as colour plate 3.

Fig. 1: *Polyommatus iranicus*, ♂, Turkey, Prov. Agri, Tahir Gecidi (HNHM)

Fig. 2: *Polyommatus "ripartii"*, ♂, Uzbekistan, vic. Tashkent, 2500 m (HNHM)

Fig. 3: *Aricia annulata*, ♂, holotype (BMNH)

Fig. 4: *Agriades kurtjohnsoni*, holotype (BMNH)

Fig. 5: *Agriades kurtjohnsoni*, paratype, ♀ (HNHM)

Fig. 6: *Agriades sikkima*, syntype (BMNH)

Fig. 7: *Albulina gaborronkayi*, holotype (BMNH) (left), paratype (BMNH) (right)

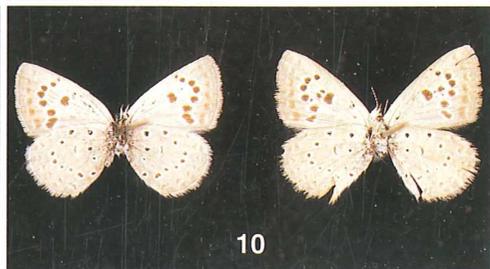
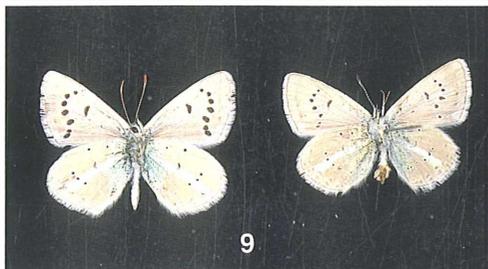
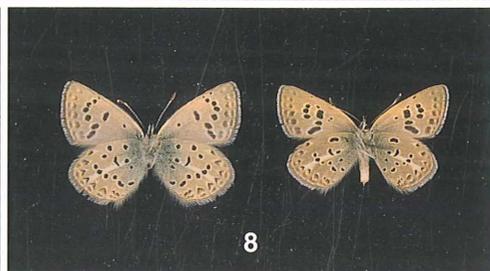
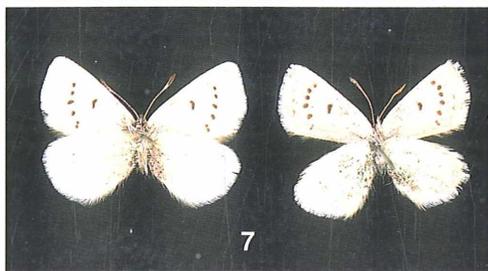
Fig. 8: *Polyommatus frauvariana*, holotype (left) and paratype ♀ (right) (NMW)

Fig. 9: *Polyommatus fabiani*, holotype (HNHM) (left), *P. wagneri*, ♂, Hasagt Hayhran, Gov'Altay, Mongolia (HNHM)

Fig. 10: *Polyommatus delessei*, holotype (MNHN) (left), paratype (HNHM) (right)

Fig. 11: *Madeleinea gradoslamsi*, paratype (HNHM) (left) and holotype (MUSM) (right)

Colour plate 4



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## **Demokratie in Deutschland oder Diktatur der Bürokraten**

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Aus diesem Grund veröffentliche ich obige Zeilen solange, bis man mir verbietet, meine Meinung über diese Demokratie und diesen Rechtsstaat zu äußern, oder bis sich couragierte, vermögende Leute finden, die gegen das Unrechtsgesetz ankämpfen bis es zurückgenommen wird.

## **Democracy in Germany or dictatorial beurocracy**

Every publisher in Bavaria is made to give two free examples of each publication to the Bavarian State Library (Munich) and a further example to the German Library (Frankfurt/Main). This was just about acceptable for me.

Since the joining of East and West Germany, we now have two national libraries, one in Frankfurt and one in Leipzig. Now the library in Leipzig is to be additionally provided with one. This I find totally unacceptable and unjust. All German literary works could be quickly gattered together in the form of a "German National Bibliography". We live in the age of data processing and computer technology, and it would be possible to build up a data base from both libraries. The BND (Germany's "Secret Service") and the "STASI" (former East Germany's "Secret Service") do not exist side by side, or do they? Two Ministries of Defence also do not exist next to one another, so why two State Libraries? The State and politicians should be setting an example to the people, and yet all they seem to do is serve themselves.

Although we live in a state where the people has the rights, it is pointless to fight such injustice. Through the beurocracy of our state and in our society, we must go from one stage to the next a bit like an obstacle course. Unless we have a good case it is pointless to spend appr DM 10,000 required to get to the finish. The chance is there naturally for those with a good case and the finance, but who has this? Those that have the money would rarely attempt this anyway. Our democracy gives us the opportunity, but our beurocracy hinders our attempts.

On these grounds I'm publishing the above statement until someone refuses to let me speak my mind or until someone with the finance makes it possible to fight the injustice.

ULF EITSCHBERGER



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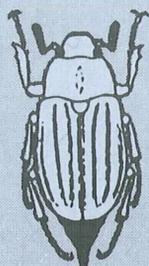
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