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Establishing criteria for higher-level classification using molecular data: the systematics of *Polyommatus* blue butterflies (Lepidoptera, Lycaenidae)

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Abstract

Most taxonomists agree on the need to adapt current classifications to recognize monophyletic units. However, delineations between higher taxonomic units can be based on the relative ages of different lineages and/or the level of morphological differentiation. In this paper, we address these issues in considering the species-rich *Polyommatus* section, a group of butterflies whose taxonomy has been highly controversial. We propose a taxonomy-friendly, flexible temporal scheme for higher-level classification. Using molecular data from nine markers (6666 bp) for 104 representatives of the *Polyommatus* section, representing all but two of the 81 described genera/subgenera and five outgroups, we obtained a complete and well resolved phylogeny for this clade. We use this to revise the systematics of the *Polyommatus* blues, and to define criteria that best accommodate the described genera within a phylogenetic framework. First, we normalize the concept of section (*Polyommatus*) and propose the use of subtribe (Polyommatina) instead. To preserve taxonomic stability and traditionally recognized taxa, we designate an age interval (4–5 Myr) instead of a fixed minimum age to define genera. The application of these criteria results in the retention of 31 genera of the 81 formally described generic names, and necessitates the description of one new genus (***Rueckbeilia* gen. nov.**). We note that while classifications should be based on phylogenetic data, applying a rigid universal scheme is rarely feasible. Ideally, taxon age limits should be applied according to the particularities and pre-existing taxonomy of each group. We demonstrate that the concept of a morphological gap may be misleading at the genus level and can produce polyphyletic genera, and we propose that recognition of the existence of cryptic genera may be useful in taxonomy.

Despite current progress in morphological and molecular studies of "Blue" butterflies, subfamily Polyommatinae (Forster, 1936, 1938; Stempffer, 1937, Stempffer, 1967; Nabokov, 1945; Eliot, 1973; Als et al., 2004; Zhdanko, 2004; Stekolnikov and Kuznetzov, 2005; Wiemers et al., 2009; Stekolnikov, 2010), their higher-level systematics remain controversial. Eliot (1973) divided this subfamily into four tribes: Lycaenesthini, Candalidini, Niphandini and Polyommatini (Table 1). Among these tribes, the Polyommatini is the most diverse and arguably one of the most systematically difficult groups of butterflies, as stated by Eliot himself: "I have to admit complete failure in my efforts to subdivide it into natural groups, simply organizing it into 30 sections" (Eliot, 1973). His division of Polyommatini into sections has nevertheless been widely accepted by the scientific community (Hirowatari, 1992; Mattoni and Fiedler, 1993; Bálint and Johnson, 1994, 1995, 1997; Io, 1998; Pratt et al., 2006; Robbins and Duarte, 2006). Some entomologists prefer considering

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Table 1
Polyommatinae classification according to Eliot (1973)

Tribe	Section	Genera
Lycaenesthini		*Lycaenesthes* Moore, 1866; *Anthene* Doubleday, 1847; *Cupidesthes* Aurivillius, 1895; *Neurypexina* Bethune-Baker, 1910; *Neurellipes* Bethune-Baker 1910; *Monile* Ungemach, 1932; *Triclema* Karsch, 1893
Candalidini		*Candalides* Hübner, 1819; *Erina* Swainson, 1833 (= *Holochila* C. Felder, 1862); *Cyprotides* Tite, 1963; *Microscena* Tite, 1963; *Adaluma* Tindale, 1922; *Nesolycaena* Waterhouse & Lyell, 1905; *Zetona* Waterhouse, 1938; *Holochila* sensu auctt. nec C. Felder
Niphandini		*Niphanda* Moore, 1875
Polyommatini		
	Cupidopsis	*Cupidopsis* Karsch, 1895
	Una	*Una* de Nicéville, 1890; *Orthomiella* de Nicéville, 1890
	Petrelaea	*Petrelaea* Toxopeus, 1929; *Pseudonacaduba* Stempffer, 1943
	Nacaduba	*Nacaduba* Moore, 1881; *Prosotas* H. H. Druce, 1891; *Ionolyce* Toxopeus, 1929; *Catopyrops* Toxopeus, 1929; *Erysichton* Fruhstorfer, 1916; *Paraduba* Bethune-Baker, 1906; *Neolucia* Waterhouse & Turner, 1905; *Hypojamides* Riley, 1929
	Theclinesthes	*Theclinesthes* Röber, 1891; *Thaumaina* Bethune-Baker, 1908; *Utica* Hewitson, 1865, invalid, praeocc.
	Upolampes	*Upolampes* Bethune-Baker, 1908; *Caleta* Fruhstorfer, 1922; *Pycnophallium* Toxopeus, 1929; *Discolampa* Toxopeus, 1929 (= *Ethion* Shirozu & Saigusa, 1962); *Pistoria* Hemming, 1964 (= *Mambara* Bethune-Baker, 1908, praeocc.)
	Danis	*Danis* Fabricius, 1807 (= *Thysonotis* Hübner, 1819; *Hadothera* Billberg, 1820; *Damis* Boisduval, 1832); *Psychonotis* Toxopeus, 1930; *Epimastidia* H. H. Druce, 1891
	Jamides	*Jamides* Hübner, 1819; *Pepliphorus* Hübner, 1819 (= *Peplodyta* Toxopeus, 1929)
	Catochrysops	*Catochrysops* Boisduval, 1832; *Rysops* Eliot, 1973
	Lampides	*Lampides* Hübner, 1819 (= *Cosmolyce* Toxopeus, 1927; *Lampidella* Hemming, 1933)
	Callictita	*Callictita* Bethune-Baker, 1908
	Uranothauma	*Uranothauma* Butler, 1895
	Phlyaria	*Phylaria* Karsch, 1895
	Cacyreus	*Cacyreus* Butler, 1898 (= *Hyreus* Hübner, 1819, praeocc.); *Harpendyreus* Heron, 1909
	Leptotes	*Leptotes* Scudder, 1876; *Syntarucoides* Kaye, 1904; *Cyclyrius* Butler, 1897; *Syntarucus* Butler, 1900 (= *Langia* Tutt, 1906, praeocc.)
	Castalius	*Castalius* Hübner, 1819; *Tarucus* Moore, 1881
	Zintha	*Zintha* Eliot, 1973
	Zizeeria	*Zizeeria* Chapman, 1910; *Zizina* Chapman, 1910; *Pseudozizeeria* Beuret, 1955
	Famegana	*Famegana* Eliot, 1973
	Actizera	*Actizera* Chapman, 1910
	Zizula	*Zizula* Chapman, 1910
	Brephidium	*Brephidium* Scudder, 1876; *Oraidium* Bethune-Baker, 1914
	Everes	*Everes* Hübner, 1819 (= *Ununcula* van Eecke, 1915); *Cupido* Schrank, 1801 (= *Zizera* Moore, 1881); *Tiora* Evans, 1912; *Bothrinia* Chapman, 1909 (= *Bothria* Chapman, 1908, praeocc.); *Tongeia* Tutt, 1908; *Shijimia* Matsumura, 1919; *Talicada* Moore, 1881; *Binghamia* Tutt, 1908

Table 1
(*Contiuned*)

Tribe	Section	Genera
	Pithecops	*Pithecops* Horsfield, 1828; *Eupsychellus* Röber, 1891
	Azanus	*Azanus* Moore, 1881
	Eicochrysops	*Eicochrysops* Bethune-Baker, 1924
	Lycaenopsis	*Lycaenopsis* C. & R. Felder, 1865; *Neopithecops* Distant, 1884; *Parapithecops* Moore, 1884; *Megisba* Moore, 1881; *Pathalia* Moore, 1884; *Arletta* Hemming, 1935 (= *Moorea* Toxopeus, 1927, praeocc.); *Celastrina* Tutt, 1906; *Notarthrinus* Chapman, 1908; *Acytolepis* Toxopeus, 1927; *Oreolyce* Toxopeus, 1927; *Monodontides* Toxopeus, 1927; *Akasinula* Toxopeus, 1928; *Ptox* Toxopeus, 1928; *Udara* Toxopeus, 1928; *Rhinelephas* Toxopeus, 1928; *Uranobothria* Toxopeus, 1928; *Parelodina* Bethune-Baker, 1904; *Vaga* Zimmerman, 1958; *Papua* Röber, 1892, invalid, praeocc.; *Cyanirioides* Matsumura, 1919, invalid, praeocc.
	Glaucopsyche	*Glaucopsyche* Scudder, 1872; *Phaedrotes* Scudder, 1876; *Scolitantides* Hübner, 1819; *Apelles* Hemming, 1931; *Philotes* Scudder, 1876; *Turanana* Bethune-Baker, 1916 (= *Turania* Bethune-Baker, 1914, praeocc.); *Palaeophilotes* Forster, 1938; *Praephilotes* Forster, 1938; *Pseudophilotes* Beuret, 1955; *Shijimiaeoides* Beuret, 1955; *Sinia* Forster, 1949; *Iolana* Bethune-Baker, 1914; *Maculinea* van Eecke, 1915; *Caerulea* Forster, 1938; *Phengaris* Doherty, 1881
	Euchrysops	*Euchrysops* Butler, 1900; *Lepidochrysops* Hedicke, 1923 (= *Neochrysops* Bethune-Baker, 1923, praeocc.); *Thermoniphas* Karsch, 1895; *Oboronia* Karsch, 1893; *Athysanota* Karsch, 1895
	Polyommatus	*Polyommatus* Latreille, 1804; *Plebejus* Kluk, 1802; *Lycaeides* Hübner, 1819; *Cyaniris* Dalman, 1816; *Nomiades* Hübner, 1819; *Aricia* R. L., 1817 (= *Gynomorphia* Verity, 1929); *Pseudoaricia* Beuret, 1959; *Kretania* Beuret, 1959; *Ultraaricia* Beuret, 1959; *Agriades* Hübner, 1819; *Vacciniina* Tutt, 1909; *Albulina* Tutt, 1909; *Bryna* Evans, 1912; *Meleageria* Sagarra, 1925; *Agrodiaetus* Hübner, 1822 (= *Hirsutina* Tutt, 1909); *Lysandra* Hemming, 1933 (= *Uranops* Hemming, 1929, praeocc.); *Plebicula* Higgins, 1969; *Eumedonia* Forster, 1938; *Plebulina* Nabokov, 1944; *Icaricia* Nabokov, 1944; *Chilades* Moore, 1881; *Edales* Swinhoe, 1910; *Luthrodes* H. H. Druce, 1895; *Freyeria* Courvoisier, 1920; *Hemiargus* Hübner, 1818; *Itylos* Draudt, 1921; *Pseudochrysops* Nabokov, 1945; *Cyclargus* Nabokov, 1945; *Echinargus* Nabokov, 1945; *Pseudolucia* Nabokov, 1945; *Paralycaeides* Nabokov, 1945; *Nabokovia* Hemming, 1960 (= *Pseudothecla* Nabokov, 1945; praeocc.); *Parachilades* Nabokov, 1945

these sections, including the Polyommatus section, as tribes (Higgins, 1975; Zhdanko, 1983). Thus the *Polyommatus* section *sensu* Eliot, 1973 is equivalent to Polyommatini *sensu* Higgins, 1975.

The *Polyommatus* section is the most species-rich group within the blue butterflies, including about 460 species. It is generally cosmopolitan, but with most genera and species restricted to the Palearctic, Neotropical and Nearctic regions. Of a total of ca. 340–350 Palearctic species, ca. 130 belong to the monophyletic *Agrodiaetus*. About 20 species occur in North America (Opler and Warren, 2004) and at least 91 in the Neotropics (Lamas, 2004). Explosive chromosome evolution has evolved independently in at least three separate lineages, *Agrodaietus*, *Lysandra* and *Plebicula* (Kandul et al., 2004). Some lineages (e.g. *Polyommatus* s.s. and *Agrodiaetus*) have extremely high rates of diversification, resulting in numerous species in these lineages despite their young age (Kandul et al., 2004, 2007). In fact, *Agrodiaetus* displays one of the highest known diversification rates in the animal kingdom (Coyne and Orr, 2004). Homoploid hybrid speciation (considered to be rare in animals) has been hypothesized in the genus *Plebejus* (Gompert et al., 2006). The group displays an interesting pattern of wing colour evolution, including multiple independent cases of discoloration, a change in colour from blue to brown (Bálint and Johnson, 1997) and rapid colour changes that may reflect reinforcement (Lukhtanov et al., 2005) or ecological adaptation (Biro et al., 2003). Studies of the biology of these butterflies have focused on evolutionary processes (Krauss et al., 2004; Lukhtanov et al., 2005; Gompert et al., 2006; Kuhne and Schmitt, 2010; Lukhtanov, 2010), ecology (Vandewoestijne et al., 2008; Rusterholz and Erhardt, 2000), biogeography (Mensi et al., 1988; Schmitt et al., 2003; Schmitt, 2007; Vila et al., 2011), conservation (Brereton et al., 2008; Vila et al., 2010), cytogenetics (White, 1973; Lukhtanov and Dantchenko, 2002; Kandul et al., 2007; Vershinina and Lukhtanov, 2010), ecological physiology (Goverde et al., 2008), physiology and genetics of colour vision (Sison-Mangus et al., 2008), climate change (Carroll et al., 2009) and symbiosis (Pierce et al., 2002; Trager and Daniels, 2009).

A robust phylogenetic framework is fundamental for the advancement of these fields of research. Several modifications have been suggested to the tentative classification proposed by Eliot in 1973 (Bálint and Johnson, 1997; Zhdanko, 2004; Stekolnikov, 2010), but no comprehensive revision has been published so far.

The systematics of the section are especially problematic at the genus level. As many as 81 genera have been described within the section, but their morphological delineations are generally unclear and a wide array of taxonomic combinations are currently in use. Two extreme approaches exist: lumpers and splitters. The lumpers include the maximum number of species in one or a few genera. Examples include the monographs by Scott (1986) and by Gorbunov (2001), where nearly all the Holarctic species of the *Polyommatus* section are lumped into a single large genus (*Plebejus*). Splitters recognize numerous genera, with a genus described for every small species group. This approach has been a common practice for the *Polyommatus* section since the work of Forster (1938). The main consequence of the taxonomy of both lumpers and splitters is the same in one respect: they generate unstructured and uninformative classifications that do not reflect evolutionary relationships between the members of the section.

For example, some researchers divided the Holarctic species into three genera: *Chilades*, *Plebejus* and *Polyommatus* (Zhdanko, 1983; Hesselbarth et al., 1995), whereas others opted for four: *Chilades*, *Plebejus*, *Aricia* and *Polyommatus* (Kudrna, 2002). This created confusion as taxa of the *Aricia*, *Eumedonia*, *Albulina*, *Agriades* and *Vacciniina* species groups are sometimes included within the genus *Plebejus* (Hesselbarth et al., 1995) and sometimes within the genus *Polyommatus* (Zhdanko, 1983).

In the past 10 years, several molecular phylogenies have been published that focused on particular genera within the *Polyommatus* section (e.g. *Agrodiaetus*—Wiemers, 2003; Kandul et al., 2004, 2007; Vila et al., 2010; *Polyommatus*—Wiemers et al., 2010), or on more general issues such as biogeography and evolution (Schmitt et al., 2003; Krauss et al., 2004; Kuhne and Schmitt, 2010; Vila et al., 2011) and DNA barcoding (Wiemers and Fiedler, 2007; Lukhtanov et al., 2009). These studies were based on the analysis of limited numbers of molecular markers and most did not contain a representative collection of all the taxa of the *Polyommatus* section. Nevertheless, together these studies showed that most genera are young and closely related, explaining the controversial systematics of the group.

A recent seven-marker phylogeny was the first detailed hypothesis published for relationships in the *Polyommatus* section (Vila et al., 2011) with special attention to New World taxa. This study revealed that all the Neotropical genera—*Pseudolucia*, *Nabokovia*, *Eldoradina*, *Itylos*, *Paralycaeides*, *Hemiargus*, *Echinargus*, *Cyclargus* and *Pseudochrysops*—together formed a well supported monophyletic clade that is sister to the Old World and Nearctic taxa. The analyses showed that all Neotropical taxa belong to the *Polyommatus* section, thus the hypothesis that the Neotropical group is polyphyletic and that several taxa belong to other sections (Bálint and Johnson, 1994, 1995, 1997) was not supported. Vila et al. (2011) also determined that the *Everes* section is sister to the *Polyommatus* section. However, this study did not include a complete sampling for the Old World taxa.

We address here the analysis of phylogenetic relationships among worldwide taxa of the *Polyommatus* section. We use a combination of three mitochondrial genes and six nuclear markers to infer phylogenetic relationships between representatives of nearly all genera, subgenera and distinct species groups described within the section. We discuss principles of taxonomic classification above the species level (subgenus, genus, section and subtribe) and propose explicit criteria for defining genera in this group. We review the importance of molecular versus morphological data in evaluating our systematic hypothesis, and propose that the recognition of "cryptic genera" may be a useful concept in taxonomy. Finally, we rearrange the classification of the *Polyommatus* section and propose a new list of genera.

Materials and methods

Taxon sampling

We used 104 representatives of the *Polyommatus* section, including at least one representative of each described genus/subgenus for all but two genera that we were unable to collect (*Xinjiangia* Huang & Murayama, 1988 and *Grumiana* Zhdanko, 2004). Four representatives for the *Everes* and one for the *Leptotes* sections were used as outgroups. All specimens used in this study are listed in Table 2. The samples (bodies in ethanol and wings in glassine envelopes) are stored in the DNA and Tissues Collection of the Museum of Comparative Zoology (Harvard University, Cambridge, MA, USA).

DNA extraction and sequencing

Genomic DNA was extracted from a leg or from a piece of the abdomen of each specimen using the DNeasy^{TM} Tissue Kit (Qiagen Inc., Valencia, CA, USA) and following the manufacturer's protocols. Fragments from three mitochondrial genes—*cytochrome oxidase I* (*COI*) + *leu-tRNA* + *cytochrome oxidase II* (*COII*); and from six nuclear markers—*elongation factor-1 alpha* (*EF-1α*), *28S ribosome unit* (*28S*), *histone H3* (*H3*), *wingless* (*Wg*), *carbamoyl-phosphate synthetase 2/aspartate transcarbamylase/dihydroorotase* (*CAD*) and *internal transcribed spacer 2* (*ITS2*) were amplified by polymerase chain reaction and sequenced as described in Vila et al. (2011). The primers employed are shown in Table S1 (Appendix S1). The sequences obtained were submitted to GenBank under accession numbers JX093196–JX093497 (Table S2, Appendix S1).

Alignment

A molecular matrix was generated for each independent marker. All sequences were edited and aligned, together with those obtained in Vila et al. (2011), using Geneious 4.8.3 (Biomatters Ltd., 2009). *ITS2* sequences were aligned according to secondary structure using the *ITS2* Database Server (Koetschan et al., 2010), as described in Schultz and Wolf (2009). The HMM-Annotator tool (Keller et al., 2009) was used to delimit and crop the *ITS2* margins (*E*-value < 0.001, metazoan HMMs), preserving the proximal stems (25 nucleotides of 5.8S and 28S rDNA). The secondary structure of *ITS2* was predicted by custom homology modelling using the template structure of *Neolysandra coelestina* (MW99013) inferred by Wiemers et al. (2010), and at least 75% helix transfer was used (ITS2PAM50 matrix; gap costs: gap open 15, gap extension 2). For the outgroup taxa in *Everes* and *Leptotes* sections, the more closely related taxa *Chilades trochylus* MW99425 and *Tarucus theophrastus* MW02025 were used, respectively, as references for secondary structure prediction. For the few cases with incomplete proximal stem (3′ end), the short missing sequence was completed using the equivalent fragment from the template. These additions were necessary to obtain a correct alignment, and were removed for the posterior phylogenetic analysis. Sequences and secondary structures were aligned synchronously with 4SALE 1.5 (Seibel et al., 2006, 2008) using an *ITS2*-specific 12×12 scoring matrix.

Regions of the matrix lacking more than 50% of data, as well as ambiguously aligned regions, were removed using Gblocks ver. 0.96 under a relaxed criterion with the following parameters: −b2 = (50% + 1 of the sequences) −b3 = 3 −b4 = 5 −b5 = all (Castresana, 2000; Talavera and Castresana, 2007). This step was not applied to the *ITS2* alignment. The final combined alignment consisted of 6666 bp: 2172 bp of *COI* + *leu-tRNA* + *COII*, 1171 bp of *EF-1α*, 745 bp of *CAD*, 811 bp of *28S*, 370 bp of *Wg*, 1069 bp of *ITS2*, and 328 bp of *H3* (see Data S1).

Phylogenetic inference and dating

Maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) were employed to estimate evolutionary relationships within Polyommatina. For MP analysis, the nine markers were concatenated in a single matrix and used as an input for the software PAUP ver. 4.0b10 (Swofford, 2000). Heuristic searches were performed with TBR branch swapping and 10 000 random taxon addition replicates, saving no more than 10 equally parsimonious trees per replicate. To estimate branch support on the recovered topology, nonparametric bootstrap values (Felsenstein, 1985) were assessed with PAUP ver. 4.0b10. One hundred bootstrap pseudoreplicates were obtained under a heuristic search with TBR branch swapping with 1000 random taxon addition replicates, saving no more than 10 equally parsimonious trees per replicate. Model-based approaches were conducted with BEAST ver. 1.6.0 (Drummond and Rambaut, 2007) for BI, and GARLI-PART ver. 0.97 (Zwickl, 2006) for ML. The data were partitioned by six markers, considering *COI* + *leu-tRNA* + *COII* a single evolutionary unit in the mitochondrial genome. jModeltest ver. 0.118 (Posada, 2008) was executed to select the best-fitting models for DNA substitution for each marker data set according to the Akaike information criterion (AIC). As a result, the HKY model was used for *H3*, the TN model for *CAD*, and a GTR model for the rest of the markers, in all cases with a gamma distribution (+G) and a proportion of invariants (+I) to account for heterogeneity in evolutionary rates among sites. The gamma distribution was estimated automatically from the data using six rate categories. Branch support was assessed by 100 bootstrap replicates for ML, and the

Table 2
Samples used in this study: taxon name, specimen label, sample accession number at MCZ and sample collection locality used in the analysis

Subtribe	Genus	Species & ssp.	Sample code	Locality
Polyommatina	*Agriades*	*glandon*	VL-05-Z994	Russia, Altai, Sailugem Range
Polyommatina	*Agriades*	*optilete optilete*	VL-01-B424	Russia, St. Petersburg, Tamengont
Polyommatina	*Agriades*	*optilete yukona*	JB-05-I879	Canada, Yukon, Dempster Hwy km 359
Polyommatina	*Agriades*	*orbitulus*	AD-03-B064	Russia, Altai, Aktash
Polyommatina	*Agriades*	*pheretiades*	NK-00-P690	Kazakhstan, Dzhambul reg., Kirgizski range
Polyommatina	*Agriades*	*podarce*	AS-92-Z130	USA, California, Leek Spring
Polyommatina	*Agriades*	*pyrenaicus dardanus*	AD-00-P259	Armenia, Gnishyk, Aiodzor Mts.
Polyommatina	*Alpherakya*	*sarta*	VL-02-X098	China, Xinjiang, Kuqa
Polyommatina	*Aricia*	*agestis*	NK-00-P712	Kazakhstan, Kayandy
Polyommatina	*Aricia*	*artaxerxes*	AD-02-W127	Russia, Primorski Krai Khanka Lake
Polyommatina	*Aricia*	*chinensis*	VL-05-Z997	Russia, Buryatia, Sosnovka, 900 m
Polyommatina	*Aricia*	*crassipuncta*	AD-00-P528	Armenia, Transcaucasus, Alibek Mt.
Polyommatina	*Aricia*	*nicias*	AD-03-B041	Russia, Altai, Aktash env.
Polyommatina	*Aricia*	*vandarbani*	VL-03-F745	Azerbaijan, Lerik, Talysh, 900–1000 m
Polyommatina	*Chilades*	*lajus*	DL-99-T242	Thailand, Prachuap Khiri Khan Province, Ampuh Thap Sakae
Polyommatina	*Cyaniris*	*semiargus belis*	AD-00-P369	Armenia, Zangezur mts., Akhtchi
Polyommatina	*Cyaniris*	*semiargus semiargus*	AD-00-P206	Russia, Low Volga, Volgograd reg., Kamytshinky
Polyommatina	*Cyclargus*	*ammon*	JE-01-C283	USA, Florida, Big Pine Key
Polyommatina	*Echinargus*	*isola*	AS-92-Z185	USA, California, Alpine, Carson River
Polyommatina	*Eldoradina*	*cyanea*	RV-05-M735	Peru, Lima, Oyón
Polyommatina	*Eumedonia*	*eumedon*	AD-03-B062	Russia, Altai, Aktash
Polyommatina	*Eumedonia*	*persephatta minshelkensis*	NK-00-P743	Kazakhstan, Shymkent reg., Karatau Mts.
Polyommatina	*Freyeria*	*putli*	RE-02-A007	Australia, Queensland, Trinity Beach
Polyommatina	*Freyeria*	*trochylus*	VL-01-L462	Turkey, Artvin, Kiliçkaya
Polyommatina	*Glabroculus*	*cyane*	VL-02-X159	Kazakhstan, Karaganda region, Aktchatau
Polyommatina	*Glabroculus*	*elvira*	NK-00-P793	Kazakhstan, Baltakul vlg.
Polyommatina	*Hemiargus*	*hanno bogotanus*	SR-03-K069	Colombia, Caldas, Chinchina
Polyommatina	*Hemiargus*	*hanno ceraunus*	MH-01-I001	Puerto Rico, Culebra Island, Flamenco Beach
Polyommatina	*Hemiargus*	*hanno gyas*	AS-92-Z255	USA, California, Los Angeles, Pyramid Lake
Polyommatina	*Hemiargus*	*hanno gyas*	DL-02-P801	USA, Arizona, Chiricahua Mts.
Polyommatina	*Hemiargus*	*huntingtoni*	RE-01-H234	Costa Rica, P.N. Santa Rosa, Guanacaste
Polyommatina	*Hemiargus*	*martha*	RV-04-I212	Peru, Huánuco
Polyommatina	*Hemiargus*	*ramon*	MFB-00-N223	Chile, Arica, Molino
Polyommatina	*Icaricia*	*acmon*	AS-92-Z184	USA, California, Alpine, Carson River
Polyommatina	*Icaricia*	*icarioides*	AS-92-Z065	USA, California, Nevada, Donner Pass
Polyommatina	*Icaricia*	*saepiolus*	AS-92-Z069	USA, California, Nevada, Donner Pass
Polyommatina	*Icaricia*	*shasta*	AS-92-Z465	USA, California, Nevada, Castle Peak
Polyommatina	*Itylos*	*huascarana*	RV-04-I403	Peru, Ancash, Pitec
Polyommatina	*Itylos*	*koa*	RV-03-V327	Peru, Junín, Huasahuasi
Polyommatina	*Itylos*	*mashenka*	MFB-00-N166	Peru, Junín
Polyommatina	*Itylos*	*sigal*	MFB-00-N220	Chile, Socoroma
Polyommatina	*Itylos*	*tintarrona*	RV-03-V182	Peru, Arequipa, Cañón del Colca
Polyommatina	*Itylos*	*titicaca*	MFB-00-N206	Chile, P.N. Lanca, Las Cuevas
Polyommatina	Kindermannia	*morgiana*	VL-02-X393	Iran, Kerman, Kuh-e-Lalizar Mts.
Polyommatina	*Kretania*	*alcedo*	VL-01-L319	Turkey, Erzurum Prov., Köprüköy
Polyommatina	*Kretania*	*eurypilus*	VL-01-L152	Turkey, Gümüshane Prov., 35 km SW Gümüshane, Dilekyolu
Polyommatina	*Kretania*	*eurypilus zamotajlovi*	SH-02-H006	Russia, Krasnodar Region, Abrau
Polyommatina	*Kretania*	*pylaon*	AD-00-P066	Russia, Volgograd, Kamyshinsky
Polyommatina	*Kretania*	*zephyrinus*	AD-00-P121	Armenia, Transcaucasus, Sevan, Shorzha
Polyommatina	*Luthrodes*	*cleotas*	CJM-07-J018	PNG, New Ireland Prov, Simberi Is.
Polyommatina	*Luthrodes*	*galba*	HU-08-D004	Cyprus, Ayios Nikolaos
Polyommatina	*Luthrodes*	*pandava*	MWT-93-A009	Malaysia, Kepong
Polyommatina	*Lysandra*	*bellargus*	AD-00-P129	Armenia, Transcaucasus, Amberd Valley, Aragatz Mt.
Polyommatina	*Lysandra*	*coridon borussia*	AD-00-P192	Russia, Tula region, Tatinki, 120 m
Polyommatina	*Lysandra*	*punctifera*	NK-02-A027	Morocco, High Atlas, Col-Tagh pass
Polyommatina	*Maurus*	*vogelii*	RVcoll09-X164	Morocco, Khenifra, S. Timahdite, Col du Zad
Polyommatina	*Nabokovia*	*cuzquenha*	RV-03-V234	Peru, Cuzco, Pisac
Polyommatina	*Nabokovia*	*faga*	MFB-00-N217	Chile, Socoroma
Polyommatina	*Neolysandra*	*coelestina alticola*	AD-00-P092	Armenia, Gegadyr, Gegamsky Mts.
Polyommatina	*Neolysandra*	*diana*	AD-00-P081	Armenia, Gegadyr, Gegamsky Mts., 1800m

Table 2
Samples used in this study: taxon name, specimen label, sample accession number at MCZ and sample collection locality used in the analysis

Subtribe	Genus	Species & ssp.	Sample code	Locality
Polyommatina	*Pamiria*	*chrysopis*	VL-05-Z998	Tajikistan, East Pamir, Sarykolski Range, Dunkeldyk Lake
Polyommatina	*Paralycaeides*	*inconspicua*	RV-03-V188	Peru, Arequipa, Cañón del Colca
Polyommatina	*Paralycaeides*	*vapa*	RV-03-V198	Peru, Puno, Chucuito
Polyommatina	*Patricius*	*lucifer*	VL-05-Z995	Russia, Altai, Chikhacheva Range, Sailugem Mt; 2300–2400 m
Polyommatina	*Plebejidea*	*loewii*	AD-00-P266	Armenia, Gnishyk, Aiodzor Mts.
Polyommatina	*Plebejus*	*anna*	AS-92-Z072	USA, California, Nevada, Donner Pass
Polyommatina	*Plebejus*	*argus*	NK-00-P135	Ukraine, Krim, Ai-Petri Mt.
Polyommatina	*Plebejus*	*argyrognomon*	AD-00-P560	Russia, Tula, Tatinki
Polyommatina	*Plebejus*	*idas armoricanella*	NK-00-P165	Russia, St. Petersburg, Luga
Polyommatina	*Plebejus*	*idas ferniensis*	NGK-02-C411	Canada, British Columbia, Castlegar
Polyommatina	*Plebejus*	*melissa*	AS-92-Z005	USA, California, Nevada, Verdi
Polyommatina	*Plebulina*	*emigdionis*	CCN-05-I856	USA, California, Kern, W. Onyx
Polyommatina	*Polyommatus*	*amandus*	NK-00-P596	Kazakhstan, Altai, Oktyabrsk
Polyommatina	*Polyommatus*	*amandus*	AD-00-P053	Russia, Volgograd region, Kamyshinsky
Polyommatina	*Polyommatus*	*amandus*	MAT-99-Q840	Spain, Pyrenees, Urús
Polyommatina	*Polyommatus*	*amandus amurensis*	AD-02-W109	Russia, Primorski Krai, S. Ussuri, Khanka Lake, Poganichnoye
Polyommatina	*Polyommatus*	*cornelia*	VL-01-L135	Turkey, Gümüshane Prov., 35 km SW Gümüshane, Dilekyolu
Polyommatina	*Polyommatus*	*damocles krymaeus*	NK-00-P103	Ukraine, Crimea, Kurortnoe
Polyommatina	*Polyommatus*	*damon damon*	MAT-99-Q841	Spain, Pyrenees, Urús
Polyommatina	*Polyommatus*	*daphnis*	NK-00-P108	Ukraine, Crimea, Kurortnoe
Polyommatina	*Polyommatus*	*dorylas armena*	AD-00-P312	Armenia, Gnishyk, Aiodzor Mts.
Polyommatina	*Polyommatus*	*erotides*	AD-03-B040	Kazakhstan, Tarbagatai Mts., Petrovskoe env.
Polyommatina	*Polyommatus*	*erschoffii*	AD-02-L274	Tajikistan, East Pamir, Sarykolski Range, Dunkeldyk Lake
Polyommatina	*Polyommatus*	*escheri*	MAT-99-Q838	Spain, Pyrenees, Urús
Polyommatina	*Polyommatus*	*glaucias*	AD-02-M278	Iran, Gorgan Prov., Shahkuh
Polyommatina	*Polyommatus*	*hunza*	VL-05-Z996	Tajikistan, East Pamir, Sarykolski Range, Dunkeldyk Lake
Polyommatina	*Polyommatus*	*icarus*	NK-00-P562	Kazakhstan, Altai, Oktyabrsk
Polyommatina	*Polyommatus*	*marcida*	AD-02-W258	Iran, Mazandaran, Geduk Pass and Veresk
Polyommatina	*Polyommatus*	*myrrha cinyraea*	AD-00-P389	Armenia, Zangezur Mts., Akhtchi
Polyommatina	*Polyommatus*	*nivescens*	MAT-99-Q904	Spain, Lleida, Rúbies
Polyommatina	*Polyommatus*	*ripartii budashkini*	NK-00-P859	Ukraine, Crimea, Karabi yaila
Polyommatina	*Polyommatus*	*stempfferi*	VL-02-X324	Iran, Esfahan, Khansar
Polyommatina	*Polyommatus*	*surakovi surakovi*	AD-00-P006	Armenia, Aiodzor mts., Gnishyk
Polyommatina	*Polyommatus*	*thersites*	MAT-99-Q947	France, Languedoc region, Mende
Polyommatina	*Polyommatus*	*thersites*	AD-00-P019	Armenia, Aiodzor Mts., Gnishyk, 1800 m
Polyommatina	*Polyommatus*	*venus*	NK-00-P810	Kazakhstan, Karzhantau vlg.
Polyommatina	*Pseudochrysops*	*bornoi*	MAC-04-Z114	Dominican Republic, Punta Cana
Polyommatina	*Pseudolucia*	*asafi*	RV-03-V020	Chile, Céspedes, Illapel
Polyommatina	*Pseudolucia*	*charlotte*	BD-02-B813	Chile, Temuco
Polyommatina	*Pseudolucia*	*chilensis*	MFB-00-N227	Chile, Farellones
Polyommatina	*Pseudolucia*	*sibylla*	RV-03-V112	Chile, Coquimbo, Río La Laguna
Polyommatina	*Pseudolucia*	*vera*	BD-02-B812	Chile, Temuco, Volcán Villarica
Polyommatina	*Rimisia*	*miris*	NK-00-P575	Kazakhstan, Altai, Oktyabrsk
Polyommatina	*Rueckbeilia*	*fergana*	NK-00-P777	Kazakhstan, Shymkent Reg., Karatau Mts., Turpan Pass
Cupidina	*Cupido*	*comyntas*	AS-92-Z312	USA, California, Davis
Cupidina	*Cupido*	*minimus*	AD-00-P540	Russia, Tula, Tatinki
Cupidina	*Talicada*	*nyseus*	JXM-99-T709	India, Karala, Trivandrum
Cupidina	*Tongeia*	*fischeri*	NK-00-P594	Kazakhstan, Altai, Oktyabrsk
Leptotina	*Leptotes*	*trigemmatus*	RV-03-V095	Chile, Coquimbo, Alcohuas

software SumTrees in the DendroPy phylogenetic Python library (Sukumaran and Holder, 2010) was used to generate a majority-rule bootstrap consensus tree.

BI with BEAST ver. 1.6.0 was used to estimate divergence times. Normally distributed tmrca priors including maximum and minimum ages from Vila et al. (2011) within the 95% HPD distribution were established on four well supported nodes, shown in Fig. 1. The resulting 95% HPD ranged from 1.5 to 3.3 Myr for node 1; from 5.5 to 13.1 Myr for node 2; from 8.4 to 16.8 Myr for node 3; and from 2.5 to 11.3 Myr for node 4. The uncorrelated relaxed clock (Drummond et al., 2006) and a constant population size under a coalescent model were established as priors. The rest of the settings and priors were set by default. Two

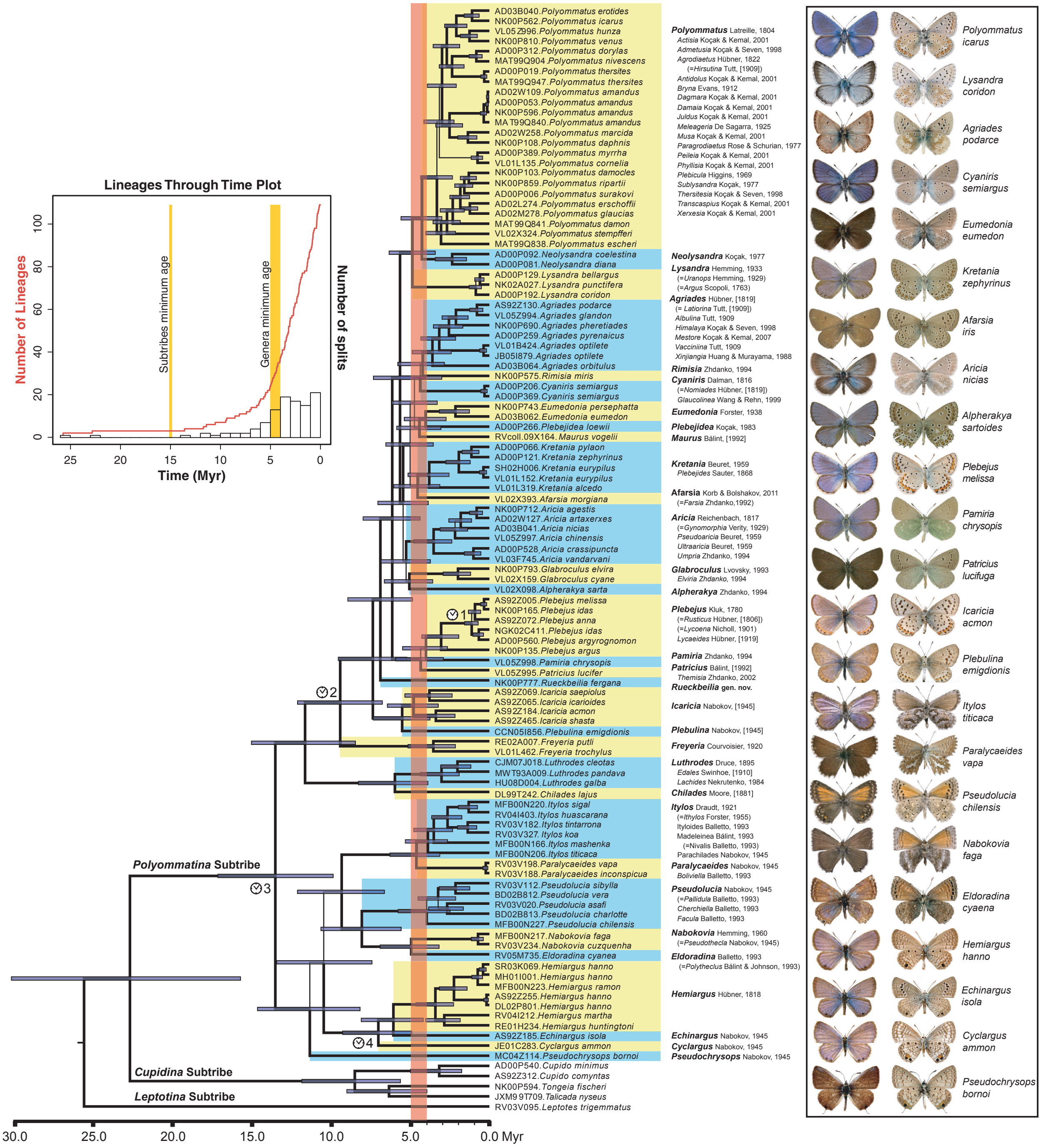

Fig. 1. Bayesian chronogram for the newly proposed subtribe Polyommatina based on nine genes: *COI*, *leu-tRNA*, *COII*, *EF-1α*, *Wg*, *ITS2*, *CAD*, *28S* and *H3* (6666 bp). Thick lines indicate supported relationships (posterior probabilities ≥ 0.95); node bars show estimated divergence times uncertainty. Nearly all the extant genera are included in the phylogeny; representatives from the subtribes Cupidina and Leptotina were used as outgroups. Valid genus names are presented in bold. Subjective synonyms (that may yet be shown to represent valid subgenera with additional research) are shown after the valid names. Objective synonyms are indicated by "=". Normally distributed tmrca from inferred divergence times in Vila et al. (2011) were used as priors on the nodes 1–4. The phylogeny revealed unexpected relationships with respect to traditional classification. We rearranged the systematics of the group and proposed a new list of genera according to the following criteria: (i) taxa older than 5 Myr are considered genera; (ii) for taxa between 4 and 5 Myr we are conservative in the sense that we consider a clade to be a genus only if it has already been described, and do not consider it a genus if it has not; and (iii) taxa younger than 4 Myr are considered subgeneric. The 4–5-Myr time interval is highlighted in red. Applying these criteria resulted in the retention of 31 of the 81 genera formally described in the group, and necessitated the addition of one new genus. Minimum age thresholds used to define genera and subtribes are indicated in the lineage through time plot. The upper side and underside of representative adult specimens of the Polyommatina are shown on the right.

independent chains were run for 50 million generations each, sampling values every 1000 steps. A conservative burn-in of 500 000 generations was applied for each run after checking Markov chain Monte Carlo (MCMC) convergence through graphically monitoring likelihood values in Tracer ver. 1.5 (Rambaut and Drummond, 2007). Independent runs were combined in LogCombiner ver. 1.6.0 implemented in the software package BEAST and all parameters were analysed using the program Tracer to determine whether they had also reached stationarity. Tree topologies were assessed using TreeAnnotator ver. 1.6.0 in the BEAST package to generate a maximum clade credibility tree of all sampled trees with median node heights. Finally, FigTree ver. 1.2.2 (Rambaut, 2009) was used to visualize the consensus tree along with node ages, age deviations and node posterior probabilities.

Ancestral states reconstruction

Character evolution was reconstructed by estimating probabilities for ancestral character states with MESQUITE ver. 2.6 (Maddison and Maddison, 2007). Both MP and ML approaches were applied to the Bayesian tree for two discrete (absence or presence) morphological characters traditionally used to define the genus *Vacciniina*: (i) metallic marginal spots on the hind wing underside; and (ii) inner apical part of the valvae in the male genitalia with sclerotized ventral fold. A reduced phylogenetic tree excluding the basal Neotropical clade and outgroup was used.

Results and discussion

Higher-level systematics

The taxonomic system employed by Eliot (1973) grouped the genera in the rather unconventional category ‘‘section’’. This system is still widely used, and it coexists with several arrangements that use the more formal categories ‘‘tribe’’ and ‘‘subtribe’’. Since this study represents the first comprehensive revision of the group since Eliot, our goal is to normalize the systematics above the level of the genus. Our phylogeny (Fig. 1) shows that the *Polyommatus* section is monophyletic (see also Vila et al., 2011). We propose to use the term ‘‘Polyommatina subtribe’’ to replace Eliot’s ‘‘*Polyommatus* section’’, and generally use the designation ‘‘subtribe’’ instead of ‘‘section’’ throughout. Thus Cupidina would be the sister to the Polyommatina, and Leptotina the sister to both. We estimate the ages of divergence for these subtribes to range between 22.8 and 25.7 Myr. In the lineages through time plot (Fig. 1), a relatively long period without diversification events, from 22.8 to 13.6 Ma, is observed. We have designated this period as a gap defining subtribes, and therefore consider subtribes to be those lineages older than 15 Myr. The three sections previously recognized by Eliot (1973) for the studied group fall within this definition of subtribe, as do most of the rest of sections in Polyommatini (Vila et al., 2011). In order to evaluate the four tribes within the subfamily Polyommatinae (e.g. Candalidini, Lycaenesthini, Niphandini and Polyommatini), an adequate threshold will need to be set for the tribal level using a more thorough phylogenetic analysis of the Lycaenidae that includes these taxa.

Genus concept

Since our aim is to establish a phylogenetically based classification system for the Polyommatina, criteria for delineating genera are important to establish. This is especially true given the wide array of taxonomic classifications that have been proposed for this group at the genus level, including drastic approaches that split the group into numerous nearly monotypic (consisting of a single species) genera (Forster, 1938; Zhdanko, 2004), or lumped all species into only a few genera (Zhdanko, 1983; Scott, 1986; Hesselbarth et al., 1995; Gorbunov, 2001; Kudrna, 2002).

Monophyly. One important criterion defining a genus is that it should be monophyletic. The majority of taxonomists currently believe that monophyly, in the narrow sense used by Hennig (Hennig, 1950, 1966; Envall, 2008; Hörandl and Stuessy, 2010) (= holophyly *sensu* Ashlock, 1971) is mandatory, at least for taxonomic categories above the species level (genus, family, etc.) (Schwenk, 1994; Groves, 2004). Paraphyletic taxa are incompatible with the principles of phylogenetic systematics (Schmidt-Lebuhn, 2011) and have relatively few defenders (Brummitt, 2003; Hörandl and Stuessy, 2010). Using paraphyletic groups in higher-level taxonomy poses serious problems as it can result in taxa that are neither mutually exclusive nor wholly inclusive of one another (Nelson et al., 2003). This gives rise to uncertainties and discrepancies in classifications. Thus avoiding paraphyletic groups and focusing on monophyletic entities *sensu* Hennig is the preferable option in practical terms. It is important to note, too, that the concept of monophyly applies to whole organisms. Trees inferred from single markers sometimes display paraphyletic relationships that reflect the evolutionary histories of individual genes rather than the species being studied. It is thus advisable to base taxonomic conclusions on multilocus analyses using the principle of character congruence as advocated by Kluge (1989) and Brower et al. (1996).

Still, the monophyly criterion alone is not enough to construct a taxonomic system. Nearly every phylogeny is a complicated structure consisting of numerous nested monophyletic lineages. The number of these nested clades is often much greater than the number of traditional taxonomic ranks. Therefore additional criteria need to be used to select which monophyletic lineages should be considered genera and which not, and similar criteria should be established for other ranks.

The morphological gap and the concept of cryptic genera. One criterion that can be used in defining a genus is the existence of a discontinuity in the distribution of morphological characters between one monophyletic group and another. The morphological gap (= morphological hiatus) seen between genera should be significantly larger than the gaps seen between species of the same genus. This criterion is widely used, but it is not ideal. First, it may be difficult to decide when a morphological gap is sufficient to separate genera (and it may be difficult to measure morphological gaps in the first place). Second, and most importantly, using this criterion can result in artificial taxonomic systems due to homoplasy. For example, the genus *Vacciniina* in its traditional conception includes three morphologically similar species: *V. optilete*, *V. alcedo* and *V. fergana* (Tuzov et al., 2000) (Fig. 2). However, our study demonstrates that these species represent three different evolutionary lineages that are not closely related (Fig. 1). In fact, we describe the new genus *Rueckbeilia* for the traditional species *V. fergana*, and include the species *V. alcedo* in the genus *Kretania* and the species *V. optilete* in the genus *Agriades*. Thus *Vacciniina sensu auctorum* represents three cryptic genera, i.e. three species clusters that cannot be separated from one another based on their morphological characters and, at the same time, cannot be lumped into a single genus as their combination would be polyphyletic. As a consequence, we suggest that the recognition of cryptic genera (Vilnet et al., 2007; Lucky and Sarnat, 2008) may be useful, in the same manner that the recognition of cryptic species is now widely used (Descimon and Mallet, 2009).

Cryptic genera are the consequence of unrecognized parallelisms in evolution of some morphological characters or of the long preservation of plesiomorphic states that are mistakenly considered synapomorphies; or of both processes acting simultaneously in different characters. For example, the species *V. optilete* seems to have independently evolved a wing pattern similar to those of *V. alcedo* and *V. fergana* (Fig. 2), whereas the "*Polyommatus*-like" structures of the male genitalia of these lineages (Stekolnikov, 2010) (Fig. 3) probably represent an ancestral condition that has been preserved for at least 6 million years (Fig. 4).

Age of lineage as a universal and unbiased criterion? Hennig (1966) proposed to synchronize taxonomic ranks universally according to geological ages. This would have the effect of making groups comparable and ranks definable. Since geological time is universal, the age of evolutionary lineages, generally estimated by the dating of nodes in phylogenetic trees, seems to be the only truly unbiased criterion by which taxonomic classifications above the level of biological species can be erected (Hennig, 1966). Avise and Johns (1999) devised a specific temporal-banding scheme to fit conventional Linnaean ranks. They proposed considering as genera those lineages that originated in the Pliocene (ca. 2–5 Ma); as subgenera the lineages above the level of species that

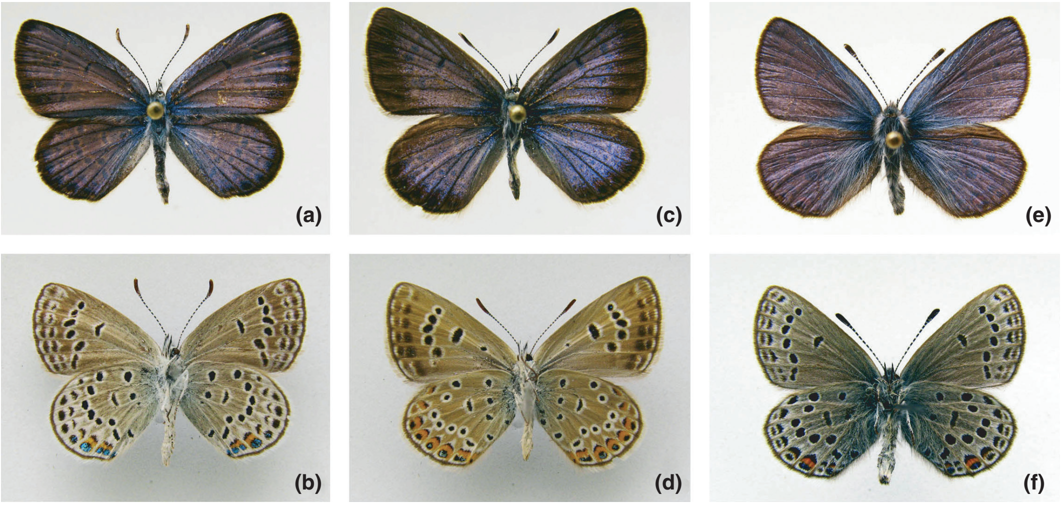

Fig. 2. Taxa representing three cryptic genera. (a,b) *Rueckbeilia fergana* (= "*Vacciniina*" *fergana*); (c,d) *Kretania alcedo* (= "Vacciniina" *alcedo*); (e,f) *Agriades optilete* (= "*Vacciniina*" *optilete*). These taxa were all considered species of the same genus (*Vacciniina*), although in fact they form three distinct genera according to the criteria described in this study. Despite their genetic differences, this artificial assemblage is strikingly convergent with respect to wing colour and pattern. They share the violet-blue colour of the wing upper side in males, and the similar wing underside with blue metallic scales that seems to have evolved independently at least twice.

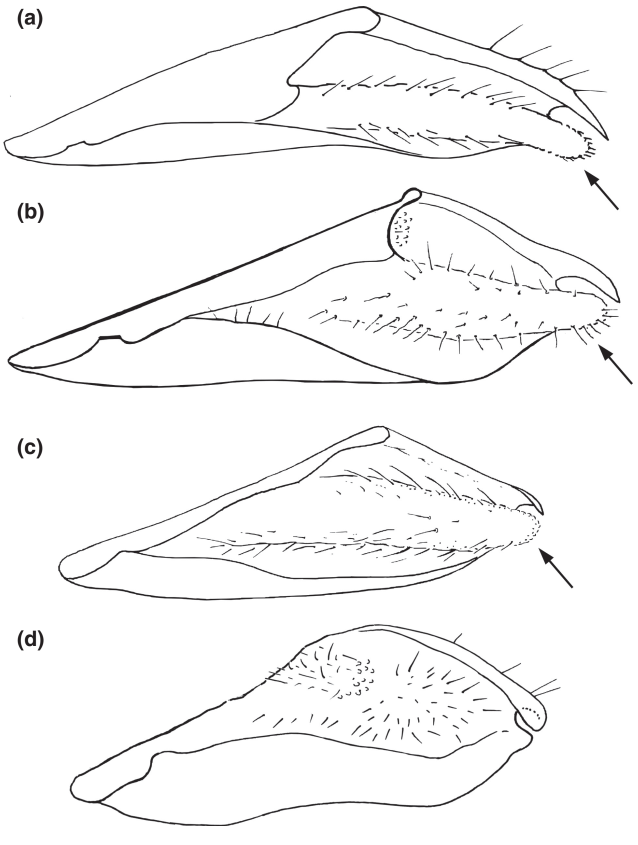

Fig. 3. Valva in the male genitalia. Inner part of valva with membranous ventral fold indicated by arrow (a–c) and without membranous ventral fold (d). (a) *Rueckbeilia fergana*; (b) *Kretania alcedo*; (c) *Agriades glandon*; (d) *Plebejus idas*. After Stekolnikov (2010) with modifications.

originated in the Pleistocene (0–2 Ma); and as tribes the lineages that originated in the Miocene (5–24 Ma).

However, this proposal has two main problems: it is not directly applicable to fossil organisms (Griffiths, 1973), and it would necessitate a major, even radical, rearrangement for current taxonomy. Acknowledging these difficulties, Avise and Mitchell (2007) launched the "timeclip proposal", which consists of labelling classic Linnaean taxa with timeclips that indicate their geological ages of origin. This could provide relevant additional information that could be updated easily without the need to alter taxonomy. Although the timeclip proposal is interesting, it still relies on a taxonomic system, and does not invalidate the need to establish true relationships within and between taxa and to decide how to determine taxonomic ranks.

We agree with the concept of relative ages, but we think this should be modified in at least two respects. First, the age thresholds must take into account the systematics and relative ages of different groups of organisms. Second, once the taxonomic ranks are established, diagnostic morphological characters should be explained or explored. Moreover, the rank of subtribe, which is especially useful in insect systematics, should be incorporated in the proposal of Avise and Johns (1999).

Stability and preservation of traditionally recognized taxa. The stability and preservation of traditionally recognized taxa must be taken into account in establishing classification guidelines (Godfray and Knapp, 2004). Indeed, stability is a concept that is positively valued by the International Commissions of Nomenclature, and that can, in some instances, take precedence over other principles. Applying a universal system of thresholds would result in taxonomic upheaval, mostly because at present there is deep discrepancy in the average age of the taxa accepted for different groups of organisms (Avise and Liu, 2011). In mammals, for example, many recognized genera are relatively young (3–5 Myr) (Castresana, 2001; Rowe et al., 2008; Abramson et al., 2009) with an estimated mean of 9.6 Myr (0.1–40) (Avise and Liu, 2011), whereas other groups may be relatively old, such as Decapoda, with an estimated mean of 60.2 Myr (16.8–135) (Avise and Liu, 2011) or Diptera (Drosophilidae, Chironomidae) with estimated means ranging from 30–40 Myr to more than 100 Myr (Avise and Johns, 1999; Cranston et al., 2010). Strong temporal banding heterogeneity among different organismal assemblages also occurs at higher taxonomic levels such as families and orders (Avise and Liu, 2011; Hedges and Kumar, 2009). Consequently, a universal system would require such a complete reorganization of the systematics of most groups of organisms that the overall effect would be deleterious to communication and understanding of taxonomic relationships.

Even if the most extreme cases, such as the relative ages of genera in Diptera or Decapoda, were to be modified to create a more balanced general classification, we propose that a temporal scheme should adapt to some degree to the particularities and pre-existing taxonomy of each group. Differences in the age thresholds might be necessarily pronounced in distantly related groups of taxa whose rates of diversification are likely to differ depending on intrinsic biological differences such as generation time and/or population size (e.g. Li, 1997), differences in the efficiency of DNA repair mechanisms (Britten, 1986), or differences in metabolic rate (Martin and Palumbi, 1993). The increased rate of nucleotide changes at several loci, including such usual phylogenetic markers as COI and CytB genes, can be affected in some phylogenetic lineages by positive selection due to their role in adaptation to specialized metabolic requirements (da Fonseca et al., 2008).

In the case of Polyommatina, the following thresholds provide a balanced classification that corresponds well with current evidence about relationships between groups: genera can be recognized as those lineages that originated in the late Miocene (older than 5 Myr), and subtribes those that originated in the early Miocene or

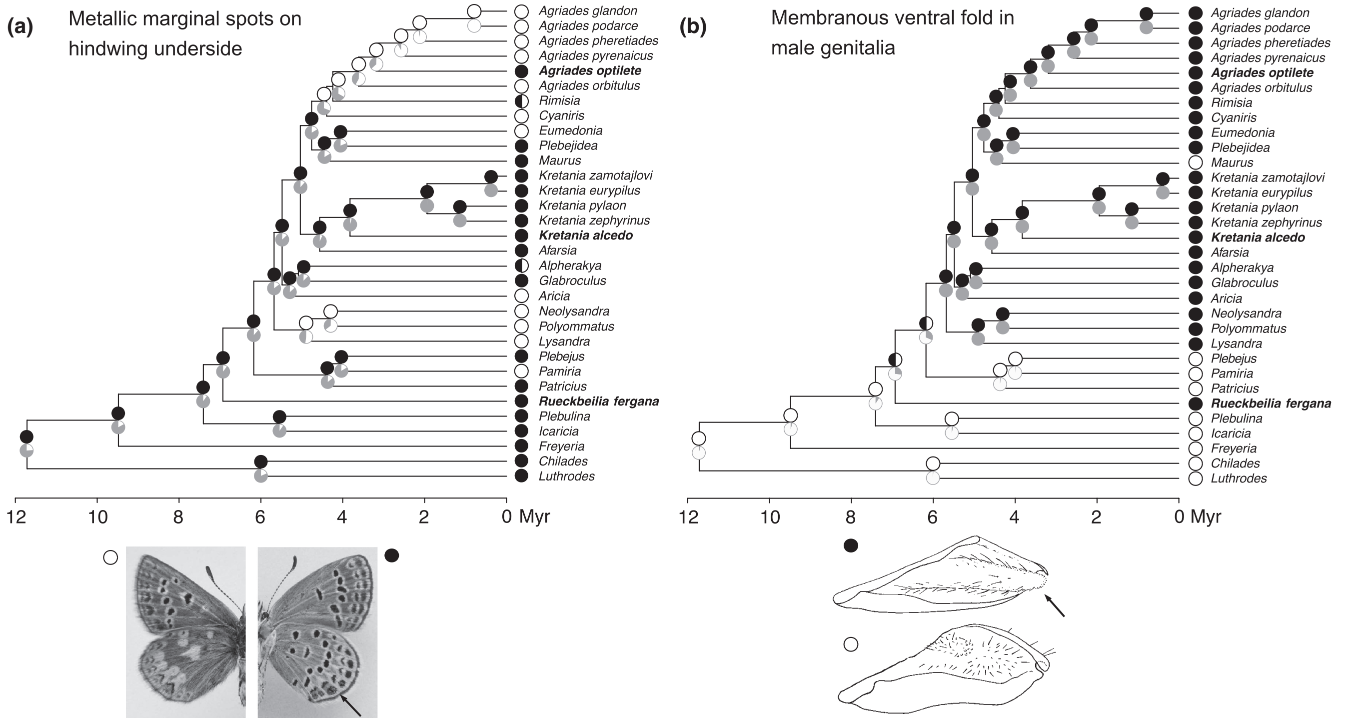

Fig. 4. Ancestral state reconstructions for two morphological characters traditionally defining the polyphyletic genus *Vacciniina* (taxa in bold). (a) Metallic marginal spots on the hind wing underside present (black circle) or absent (white circle). (b) Inner part of valvae in the male genitalia with membranous ventral fold (black circle) or without membranous ventral fold (white circle). Maximum parsimony (upper circles) and Maximum likelihood (lower grey circles) inferences are represented at nodes. Figures of genitalia are given after Stekolnikov (2010).

late Oligocene (older than 15 Myr). In the lineages through time plot, an increase in diversification can be seen starting at 5–4 Ma (Fig. 1), so we set the minimum age for genera at this point to avoid excessive splitting. This approach (plotting the number of lineages or branching events over time) is useful to illuminate diversification patterns in the group under study. Substantial changes in the rate of diversification mark key moments in the evolution of a group as a whole, and these are logical points to be used as age thresholds delimiting taxonomic ranks.

In our case, age thresholds were also selected so as to minimally affect the existing nomenclature and avoid the need for descriptions of new genera. A generic threshold of 3–4 Myr requires the creation of two new genera (the splitting of *Icaricia* and description of the new *Rueckbeilia*), while a 5–6 Myr threshold would have entailed a wide-scale synonymization (50 subjective synomyms) with excessive loss of phylogenetic information, and would have still required the description of *Rueckbeilia*. Wider thresholds would have also involved losing substantial input from the molecular data.

Accounting for uncertainty in age estimates. Additionally, any system of classification should recognize the uncertainty inherent in estimating evolutionary age given intrinsic errors associated with the methods of inference, especially when no paleontological material is available to calibrate a molecular clock. Absolute age is likely to vary depending on the analysis, and new information helping to calibrate the molecular clock, or additional methodological improvements, might affect age estimates. In contrast, relative ages among lineages are less affected by these factors because they do not depend on external information for tree calibration. The greater uncertainty in absolute age estimates compared with those based on relative ages is another reason to apply a temporal scheme specific to the group being studied, which could be adapted eventually to a different molecular substitution rate without major implications for the taxonomy of the group. A universal temporal scheme would suffer from taxonomic instability caused by uncertainty in absolute age, which is necessary when comparing taxa that are not closely related to each other. Divergent lineages sometimes display disparate molecular substitution rates, whereas closely related taxa tend to be more uniform in this regard (Martin and Palumbi, 1993; Li, 1997). The subtribe Polyommatina, a clade that evolved ca. 22.8 Ma, contains many taxa to be compared, but these are sufficiently evolutionarily and ecologically similar that they do not exhibit excessive variability in substitution rates among lineages.

In order to reduce the effect of the uncertainty in age estimates, and to avoid taxonomic instability because of small differences obtained using different phylogenetic analyses and/or novel calibration points, we propose using a time interval to set the limits of genus age, rather than a single date (e.g. 4.0–5.0 Myr for genus minimum age in our case). Thus lineages with a mean age within these intervals can be dealt with using this relatively conservative approach, as described below.

Importance of morphological diagnostic characters. Once the classification of a group is produced using the previously discussed criteria, the next critical step is to explore and explain the diagnostic morphological characters that define the proposed taxa. The exercise of integrating the molecular-based classification into a morphological framework has multiple benefits. It does not create a discontinuity with the previous morphology-based classifications; it avoids wasting the morphological data painstakingly gathered; and it allows for the reinterpretation of earlier work. It also facilitates the placement of extinct taxa and those that have not yet been sequenced, and overcomes the major drawback of a system based purely on molecular data.

Genera within the Polyommatina. In practice, we apply these criteria in the following manner.

1. We define as genus any lineage older than 5.0 Myr.
2. Between 4.0 and 5.0 Ma we are conservative, in the sense that we consider a clade to be a genus only if it has already been described, and do not consider it a genus if it has not.
3. We lump into another genus any lineage younger than 4.0 Myr.

Applying this taxonomy-friendly, flexible temporal scheme to the phylogeny and dating produced the division of the subtribe Polyommatina into 32 genera (Table 3). From this classification scheme, one new genus needs to be described and 39 names can be regarded as subjective synonyms or valid subgenera. The further designation of these 39 taxa as either subgenera or subjective synonyms requires additional data for all the species that each one represents, which is beyond of the scope of this paper.

For the 32 established genera, monophyly was statistically supported for the three phylogenetic methods used, with the sole exception of *Kretania*, where the phylogenetic position of *K. alcedo* was not resolved in the MP analysis (Table 3).

Composition and phylogenetic relationships of genera in the *Polyommatina*: before and after this study.

The nine-marker phylogeny revealed that the subtribe Polyommatina includes two major clades: the Neotropical clade (the genera *Pseudolucia*, *Nabokovia*, *Eldoradina*, *Itylos*, *Paralycaeides*, *Hemiargus*, *Echinargus*, *Cyclargus* and *Pseudochrysops*) and the non-Neotropical clade (the remaining genera).

The Neotropical clade. Relationships within the Neotropical clade have already been discussed in detail in a previous publication (Vila et al., 2011). Briefly, the Neotropical taxa are divided into four well supported clades. Two of these, probably sister clades, are formed by Andean, typically high-altitude taxa that occur south of Central Colombia. These are *Eldoradina* Balletto, 1993, *Nabokovia* Hemming, 1960 and *Pseudolucia* Nabokov, 1945 on one hand; and *Itylos* (= *Madeleinea* Bálint, 1993) and *Paralycaeides* Nabokov, 1945 on the other. The other two clades are formed by lowland taxa, including all the Caribbean representatives and species occurring north of Central Colombia, plus a few with more southern distributions. One clade is formed by *Cyclargus* Nabokov, 1945; *Echinargus* Nabokov, 1945 and *Hemiargus* Hübner, 1818; the other by *Pseudochrysops* Nabokov, 1945. The position of *Pseudochrysops* with respect to the other three clades is unresolved, probably due to its early divergence and very long branch.

The non-Neotropical clade. The non-Neotropical clade of the subtribe Polyommatina is strongly asymmetrical, with multiple nested lineages that are discussed below.

Chilades–Luthrodes clade. Within the non-Neotropical clade, *Chilades* Moore, [1881] (TS: *Papilio lajus* Stoll, [1780]) and *Luthrodes* Druce, 1895 (TS: *Polyommatus cleotas* Guérin-Méneville, [1831]) form a clade that is sister to the rest. The age of divergence between these two groups is 6.0 Myr, thus we consider them good genera despite the fact that most recent studies (Bridges, 1988) have lumped them together. Representatives of both *Chilades* and *Luthrodes* have a similar, most likely plesiomorphic, pattern on the wing underside with the presence of all the basic elements typical of the non-Neotropical Polyommatina. However, the male genitalia in *Luthrodes* are very distinct—clearly different from those in other genera—in the shape of the valvae, which are broad and trapeziform, and in the presence of a dorsal process at the distal end of the valvae that is markedly elongated and directed downwards (Bethune-Baker, 1913; Zhdanko, 1983, 2004; Stekolnikov and Kuznetzov, 2005). Within *Luthrodes*, the taxa *Edales* Swinhoe, [1910] (TS: *Lycaena pandava* Horsfield, [1829]) and *Lachides* Nekrutenko, 1987 (TS: *Lycaena galba* Lederer, 1855) are aged less than 4.0 Myr, and consequently should be considered subjective synonyms or subgenera of *Luthrodes*. However, this question may be better assessed after a study including additional species.

Bethune-Baker (1913) studied the male genitalia of *Chilades lajus* and showed that, unlike *Luthrodes*, the valvae are elongated and have a short dorsal process. In fact, the genital morphology of *Chilades* is more similar to that of *Freyeria* than to *Luthrodes*.

Table 3
Posterior probabilities and bootstrap values for monophyly in BI/ML/MP inferences, ages (mean and stdev), number of species, and larval food plant families for the 32 genera within the subtribe Polyommatina

Genus	Monophyly stability values	Genus age (Myr)	Number of species	Food plant
Polyommatus	100/100/100	4.3 [3.0–5.6]	183	Fabaceae
Neolysandra	100/100/100	4.3 [3.0–5.6]	6	Fabaceae
Lysandra	100/100/100	4.9 [3.4–6.4]	15	Fabaceae
Aricia	100/100/99	5.3 [3.7–6.9]	15	Geraniaceae
Glabroculus	100/100/100	5.1 [3.6–6.7]	2	Limoniaceae
Alpherakya	Single specimen	5.1 [3.6–6.7]	5	Crassulaceae
Agriades	100/73/81	4.2 [2.9–5.8]	19	Primulaceae, Saxifragaceae, Ericaceae Fabaceae
Rimisia	Single specimen	4.2 [2.9–5.8]	1	Fabaceae
Cyaniris	100/100/100	4.4 [3.0–5.7]	2	Fabaceae
Eumedonia	100/100/100	4.0 [2.7–5.4]	3	Geraniaceae
Plebejidea	Single specimen	4.0 [2.7–5.4]	2	Fabaceae
Maurus	Single specimen	4.4 [3.1–5.9]	1	Geraniaceae
Kretania	99/77/–	4.6 [3.1–6.1]	17	Fabaceae
Afarsia	Single specimen	4.6 [3.1–6.1]	9	Fabaceae
Plebejus	100/99/98	4.0 [2.7–5.5]	40	Fabaceae, Elaeagnaceae Empetraceae Ericaceae
Pamiria	Single specimen	4.0 [2.7–5.5]	7	Unknown
Patricius	Single specimen	4.4 [2.9–5.9]	7	Unknown
Rueckbeilia	Single specimen	6.9 [4.9–9.0]	2	Fabaceae
Icaricia	96/66/99	5.5 [3.8–7.4]	7	Polygonaceae Fabaceae
Plebulina	Single specimen	5.5 [3.8–7.4]	1	Chenopodiaceae
Freyeria	100/100/100	9.5 [6.8–12.2]	3	Boraginaceae, Phyllanthaceae, Fabaceae
Luthrodes	100/100/100	6.0 [3.9–8.3]	9	Fabaceae Cycadaceae
Chilades	Single specimen	6.0 [3.9–8.3]	ca. 12	Rutaceae Tiliaceae
Pseudolucia	100/100/98	8.1 [5.6–10.7]	46	Fabaceae Polygonaceae Portulacaceae Cuscutaceae
Nabokovia	100/100/100	5.0 [3.2–6.9]	3	Fabaceae
Eldoradina	Single specimen	5.0 [3.2–6.9]	2	Unknown
Itylos	99/74/76	4.6 [3.1–6.3]	24	Fabaceae
Paralycaeides	100/100/100	4.6 [3.1–6.3]	3	Fabaceae
Hemiargus	100/100/100	6.1 [4.2–8.1]	ca. 5	Fabaceae Cucurbitaceae Oxalidaceae
Echinargus	Single specimen	6.1 [4.2–8.1]	1	Fabaceae
Cyclargus	Single specimen	7.0 [4.9–9.3]	7	Asteraceae Fabaceae Malpighiaceae Sapindaceae
Pseudochrysops	Single specimen	11.4 [8.2–14.7]	1	Unknown

Freyeria clade. *Freyeria* Courvoisier, 1920 (TS: *Lycaena trochylus* Freyer, 1845) is frequently treated by modern authors as a subgenus of *Chilades* (Bálint and Johnson, 1997; Tolman and Lewington, 1997). Valvae in the male genitalia of *Freyeria* are elongated and have a short dorsal process (Zhdanko, 2004), and are generally similar to those of *Chilades*. However, molecular data demonstrate that *Freyeria* is not closely related to *Chilades* and represents a distinct clade that cannot possibly be subsumed within *Chilades* as it would result in a paraphyletic assemblage.

Our analysis includes one specimen of *Freyeria* from Turkey (*F. trochylus*) and one from Australia (*F. putli* (Kollar, [1844])). The taxon *F. putli* has until recently been considered a subspecies of *F. trochylus* (Common and Waterhouse, 1981; Parsons, 1999), but now most authors treat it as a good species (Bálint and Johnson, 1997; Braby, 2000). In our analysis, *F. trochylus* and *F. putli* appear as sister taxa, and we estimate that they diverged ca. 3.6 Ma. This is a surprisingly old divergence, and supports the recognition of *F. putli* as a distinct species.

Icaricia–Plebulina clade. In the original descriptions of the genera *Icaricia* Nabokov, [1945] (TS: *Lycaena icarioides* Boisduval, 1852) and *Plebulina* Nabokov, [1945] (TS: *Lycaena emigdionis* Grinnell, 1905), the author clearly indicated morphological characters that distinguished these genera from all other lycenids. In particular, Nabokov noted that *Plebulina* remarkably amalgamates the form of aedeagus similarly to *Plebejus*, with uncus, subunci, and valvae similar in shape to those found in *Albulina*. On the other hand, *Icaricia* remarkably combines a wing pattern similar to that of *Plebejus* with a shape of aedeagus similar to that found in *Aricia* (Nabokov, 1945). Since their description, however, the genera *Icaricia* and *Plebulina* generally have been treated as junior subjective synonyms, or as subgenera of either *Aricia* Reichenbach, 1817 or *Plebejus* Kluk, 1780 (Scott, 1986; Bálint and Johnson, 1997; Gorbunov, 2001; Brock and Kaufman, 2003; Opler and Warren, 2004). In all our analyses, the taxa within *Icaricia* and *Plebulina*, as well as the taxon *Lycaena saepiolus* Boisduval, 1852, form an exclusively Nearctic clade that is sister to all the rest of the Holarctic taxa. Such a topology in the phylogeny is unexpected given modern taxonomic treatments of these groups, and implies that *Icarica* and *Plebulina* cannot possibly be included within *Plebejus* or *Aricia*. This strongly supported result confirms that of Vila et al. (2011), who showed that this clade is the result of a relatively old colonization of the New World that occurred ca. 9.3 Ma. The age of divergence of *Icaricia* (including the taxon *I. saepiolus*) from the *Plebulina* lineage is 5.5 Myr. As a consequence, we maintain the monotypic *Plebulina* as a separate genus, a decision reinforced by the fact that *P. emigdionis* Grinnel, 1905 feeds on a different host-plant family (Chenopodiaceae) from the *Icaricia* taxa (Fabaceae and Polygonaceae), and by certain peculiarities of its larval morphology (Ballmer and Pratt, 1988). Interestingly, divergence ages within the *Icaricia* lineage are fairly old, reaching 4.8 Myr for the *I. acmon–I. shasta* versus *I. icarioides–I. saepiolus* split, which still falls within the 4.0–5.0 Myr genus timeframe. Since no separate genus name has ever been proposed for the *I. acmon–I. shasta* clade, we conservatively retain *Icaricia* as a single unit.

The genus Rueckbeilia (= "Vacciniina" fergana clade). The next well supported lineage found in our analysis is represented by a single species traditionally known as *Vacciniina fergana*. This species is recovered as sister to the rest of the Holarctic taxa, except for the *Icaricia–Plebulina* clade. This result is unexpected (but see Kandul et al., 2004; Lukhtanov et al., 2009) as the external morphology of *V. fergana* is extremely similar to *V. optilete*, the type-species of *Vacciniina*. This position of *V. fergana* in the phylogeny is strongly supported in all the analyses and thus cannot be considered an artifact. The deep divergence of the *V. fergana* lineage (6.9 Ma) indicates that it should be treated as a distinct genus, which we describe in the Appendix 1 under the name ***Rueckbeilia* gen. nov.** Interestingly, the isolated systematic position of *V. fergana* was not apparent in a detailed morphological study of this species (Stekolnikov, 2010). In fact, *V. fergana* exhibits a combination of primitive male genitalic characters that are found in some other taxa (Stekolnikov, 2010), and wing patterns that may represent a plesiomorphic condition in *Rueckbeilia*, *Glabroculus* and *Afarsia* + *Kretania*, but independently evolved in *Agriades optilete* (Fig. 4). A more detailed description of *Rueckbeilia* is given in the Appendix 1.

Patricius + (*Pamiria* + *Plebejus*) clade (lineage of *Plebejus sensu lato*). The grouping *Patricius* + (*Pamiria* + *Plebejus*) is recovered as a well supported clade in our phylogeny. This result is not trivial, as *Patricius* and *Pamiria* have usually been regarded as closely related to *Albulina* (Bálint and Johnson, 1997). However, the close relationship of *Patricius* (TS: *Lycaena lucifera* Staudinger, 1867), *Pamiria* (TS: *Lycaena chrysopis* Grum-Grshimailo, 1888) and *Plebejus* (TS: *Papilio argus* Linnaeus, 1758) had already been recognized by Zhdanko (2004), who noted that these genera shared similar *Plebejus*-like male genitalia. Within this clade, the genus *Patricius* is sister to the rest (divergence age 4.4 Myr), while *Pamiria* and *Plebejus* diverged 4.0 Ma.

In all our analyses, the studied species of *Lycaeides* Hübner [1819] (TS: *Papilio argyrognomon* Bergstrasser [1779], also includes *idas*, *melissa* and *anna*) form a clade that is sister to *Plebejus argus*, but its recent age (3.1 Myr) recommends the inclusion of *Lycaeides* within *Plebejus*. Noticeably, Nearctic *Lycaeides* representatives appear as polyphyletic, with unexpected, yet strongly supported, sister relationships between Old and New World taxa. This result is similar to that obtained independently by other researchers (Nice et al., 2005; Gompert et al., 2008; Vila et al., 2011) and deserves further analysis. A number of authors consider *Agriades*, *Alpherakya*, *Vacciniina*, *Plebejides* and *Plebejidea* as synonyms or subgenera of *Plebejus* (Bálint and Johnson, 1997; Gorbunov, 2001), but our results show that these taxa are more closely related to *Aricia* and *Polyommatus* than they are to *Plebejus*. Thus the prevalent use of *Plebejus* as a supergenus is not possible according to the recovered topology.

Polyommatus sensu lato clade. The rest of the Polyommatina taxa form a large clade consisting of 14 genera from *Alpherakya* to *Polyommatus* (Fig. 1). It corresponds to *Polyommatus sensu* Zhdanko, 1983 (but not to *Polyommatus sensu* Zhdanko, 2004) and can be defined by characters of male genitalia similar to those of *Polyommatus sensu stricto* (Zhdanko, 1983, 2004).

However, these genitalic characters may not constitute a true synapomorphy. Stekolnikov (2010) demonstrated a degree of heterogeneity in the male genitalia of this group, and a similar type of genitalia was found in *Rueckbeilia fergana*, which is not closely related. While the *Polyommatus sensu lato* clade is strongly supported, it is formed by several subclades that are older than 4 Myr. The evolutionary relationships among these supported subclades are in some cases unresolved, and we will discuss each in the following paragraphs.

The genus Alpherakya. *Alpherakya* Zhdanko, 1994 (TS: *Lycaena sarta* Alpheraky, 1881) is recovered as sister to *Glabroculus*, although this relationship is not well supported. It should also be noted that the wing patterns and food plants of these two taxa are different (Table 3). The morphology of this genus is characterized by a unique combination of traits that make its identification unmistakable. *Alpherakya* differs from all genera of the *Polyommatus sensu lato* clade, except for *Lysandra*, in having chequered wing fringes. It differs from *Lysandra* in having hairs on the eyes that are scarce and short, whereas in *Lysandra* they are long and dense. In male genitalia, the structure of the valvae is also diagnostic: valvae are comparatively short and broad, with a robust sclerotized inner fold, with a spade-shaped dorsal element in the apex and sclerotized ventral elements. *Alpherakya* can be separated from the taxa in the *Patricius* + (*Pamiria* + *Plebejus*) clade by the wide uncus (Zhdanko, 2004) and by the structure of valvae (Fig. 4). The larval food plants of the *Alpherakya* species are also peculiar: they feed on Crassulaceae (Zhdanko, 1997), whereas most species and genera of the subtribe Polyommatina are associated with Leguminosae or Geraniaceae. Bálint and Johnson (1997) considered *Alpherakya* as part of the genus *Plebejus*. However, our analysis, like the morphological analysis by Zhdanko (2004), does not support this hypothesis and demonstrates that these two genera are phylogenetically distant.

Glabroculus clade. Zhdanko (2004) synonymized *Glabroculus* Lvovsky, 1993 (TS: *Lycaena cyane* Eversmann, 1837) with *Plebejidea*, and considered *Elviria* (TS: *Lycaena elvira* Eversmann, 1854) to be a subgenus of *Plebejidea*. Bálint and Johnson (1997) considered *Glabroculus* (= *cyane*-group) as part of the genus *Polyommatus sensu lato*. Our data support none of these hypotheses. We show that neither *Plebejidea* nor *Polyommatus* is closely related to *Glabroculus*. Instead, *Glabroculus* appears as a sister to *Alpherakya*, although with low statistical support.

Morphologically, *Glabroculus* differs from *Polyommatus* by hairs on the eyes that are scarce and short (in *Polyommatus* they are long and dense) and by the presence of metallic marginal spots on the underside of hind wings. *Glabroculus* differs from the phylogenetically most closely related genus, *Alpherakya*, in having unchequered wing fringes. Moreover, the food plants of *Glabroculus* and *Alpherakya* are different (Table 3). The taxon *E. elvira* (the type-species of the nominal genus *Elviria*) was recovered as a sister to *G. cyane*, and the time of their divergence was estimated as ca. 2.0 Mya. Therefore *Elviria* can be considered a synonym of *Glabroculus*.

Aricia clade. The taxa representing *Aricia* (TS: *Papilio agestis* Denis & Schiffermüller, 1775) and *aratxerxes)*, *Umpria (*TS: *Lycaena chinensis* Murrey, 1874*)*, *Pseudoaricia* (TS: *Polyommatus nicias* Meigen, 1829) and *Ultraaricia* (TS: *Lycaena anteros* Freyer, 1839; includes the studied species *crassipuncta* and *vandarbani*) form a strongly supported clade. Since the divergences among them are younger than 4 Myr, the three latter taxa are subsumed within *Aricia*. The position of *Aricia* within the Polyommatini has been a subject of much discussion. Bálint and Johnson (1997) considered *Aricia* as closely related to the Neotropical taxon *Madeleinea*. Zhdanko (2004) also considered *Aricia* as one of the most basal within the *Polyommatus* section. In contrast, Stekolnikov (2010) found it to represent a young lineage closely related to *Polyommatus*. Our molecular data support the latter hypothesis, although the position of *Aricia* within the *Polyommatus sensu lato* clade is unresolved. Indeed, we recover *Aricia* as sister to *Alpherakya* + *Glabroculus*, but with low support.

Morphologically the genus is quite distinct. In the male genitalia, the aedeagus is lanceolate, with caulis developed, and entirely sclerotized, which is not observed in other taxa of the subtribe (Zhdanko, 2004). Among external characters, the naked eyes and absence of metallic spots on the underside of hindwings are characteristic, although they are not unique within the subtribe.

The genus Afarsia. (TS: *Cupido hyrcana* Lederer, 1869—an invalid name; the valid synonym is *Cupido morgiana* Kirby, 1871). The taxon *C. morgiana* was recognized as a distinctive entity by Zhdanko (1992, 2004) and Bálint and Johnson (1997), but its relationships with other taxa have never been properly documented. Bálint and Johnson (1997) placed it in the same group as *Patricius*, *Pamiria*, *Plebejidea*, *Vacciniina* and *Albulina*. In our reconstruction, it is recovered as sister to *Kretania*, but the support for this relationship is low. Its rather deep divergence (4.6 Myr) suggests that it should be treated as an independent genus. The genus name *Farsia* Zhdanko, 1992, for which *C. morgiana* is the type species, was preoccupied and the new name *Afarsia* Korb and Bolshakov, 2011 (= *Farsia* Zhdanko, 1992; nec *Farsia* Amsel, 1961) has recently been proposed as replacement (Korb and Bolshakov, 2011).

The morphology of the male genitalia of the genus *Afarsia* is similar to *Kretania sensu lato* (see below), but these two taxa are distinct in wing pattern: in *Afarsia* a discal spot on the fore wing upper side is always present and usually strongly enlarged, and one of the marginal metallic spots of the hind wing underside is enlarged. These characters of the wing pattern are also found in the genus *Albulina* (that was the reason why some authors placed *Afarsia* within or close to *Albulina*—see above). However, male genitalia in *Afarsia* are considerably different from those in *Albulina*, both in the structure of uncus, which is basally narrow with long slender arms, and in the shape of the valvae, which have a characteristically concave dorsal margin (Zhdanko, 2004).

Kretania clade. In all our analyses, the taxa within *Plebejides* (TS: *Lycaena pylaon* Fischer von Waldheim, 1832 and *P. zephyrinus*) and *Kretania sensu stricto* (TS: *Lycaena psylorita* Freyer, 1845, includes the studied species *K. eurypilus* and *K. zamotajlovi*), as well as the species *V. alcedo*, form a distinct, statistically well supported clade in ML and BI analyses that originated 4.6 Mya and should be considered as a genus. Within this genus, the species *V. alcedo* appears as sister to the rest, although the position of this taxon is unresolved in the MP analysis. The statistical support for the subclade *Kretania* s.s. + *Plebejides* is very high (100/100/100) and the time of divergence of this subclade is quite recent (ca. 1.9 Mya). The close relationship of *Kretania* s.s. and *Plebejides* was first suggested by Wiemers (2003) based on the molecular analysis of *COI* barcodes and nuclear *ITS2*. Interestingly, the close relationship between *V. alcedo*, *Kretania* s.s. and *Plebejides* has never been recognized by morphologists, who usually consider them as members of different, not closely related groups: *Plebejides* as a member of the *Plebejus* lineage (Zhdanko, 1983; Bálint and Johnson, 1997), *Kretania* as a member of the *Polyommatus* lineage (Bálint and Johnson, 1997), and the taxon *V. alcedo* as a species of *Vacciniina* (Bálint and Johnson, 1997). Nevertheless, these butterflies are fairly similar phenotypically. In fact, species of *Kretania* s.s. differ from *Plebejides* and *V. alcedo* largely in discoloured (brown) upper wings in males, but this is a labile character that has low value in genus-level taxonomy, as it seems to have evolved independently numerous times in the evolution of the Polyommatina (Bálint and Johnson, 1997; Lukhtanov et al., 2005). As a result, we propose the following new combinations: *Kretania alcedo* **comb. nov.**, *Kretania pylaon* **comb. nov.**, *Kretania zephyrinus* **comb. nov.**

The structure of the valvae in *Kretania sensu lato* (including *Plebejides* and the taxon *K. alcedo*) is typical of the genera *Polyommatus* or *Aricia* (Stekolnikov, 2010) (but not typical of the genus *Plebejus* as suggested by Zhdanko, 2004), the uncus is narrow (Zhdanko, 2004) and the wing pattern is extremely similar to that found in *Plebejus*. The combination of these morphological characters makes the genus *Kretania sensu lato* quite distinct.

The genus Maurus. The north African endemic species *Lycaena vogelii* Oberthür, 1920 has been included either within *Plebejus* or in the monotypic genus *Maurus* Bálint, [1992]. Our analysis recovers it as sister to the *Plebejidea–Eumedonia* clade with low support, but its age (4.4 Myr) is sufficient to maintain the genus *Maurus*. The morphology of the genitalia of *M. vogelii* has been described as close to that of *Plebejus* (Zhdanko, 2004). The external morphology of the genus is distinctive and can be recognized by the combination of chequered wing fringes and strongly enlarged discal spot on the fore wing upper side.

Plebejidea–Eumedonia clade. The genus *Plebejidea* (TS: *Lycaena loewii* Zeller, 1847) is usually considered to be close to *Glabroculus* (Tuzov et al., 2000; Zhdanko, 2004), *Polyommatus* (Bálint, 1991), or *Albulina* (Bálint and Johnson, 1997). Our data support none of these taxonomic hypotheses. Instead, in our reconstruction, *Plebejidea* appears as sister to *Eumedonia* with high statistical support. This result is unexpected, as representatives of *Plebejidea* and *Eumedonia* clearly differ in wing pattern and coloration and also in ecology: the species of *Eumedonia* inhabit humid biotopes and their larval food plants are species of Geraniaceae, whereas the species of *Plebejidea* inhabit very dry semi-desert biotopes and their larval food plants are xerophilous species of *Astragalus* (Fabaceae). The morphology of the male genitalia in *Plebejidea* is similar to that of *Glabroculus* (Zhdanko, 2004), but differs by a noticeable basal sclerotization of the subcostal groove of the valvae (Stekolnikov, 2010).

The genus Eumedonia. (TS: *Papilio eumedon* Esper, [1780]) has been considered to be close to *Aricia* (Bálint and Johnson, 1997; Tuzov et al., 2000) in part because they share the same larval food plants (Geraniaceae). However, our results do not support this close relationship, and differences in the structure of the uncus in the male genitalia (Zhdanko, 2004) also suggest that these genera are not closely related. In fact, the genus *Eumedonia* is morphologically quite distinct. It shares a similar form of the valvae in male genitalia with *Plebejidea*, the phylogenetically most closely related genus, as well as with the more distant *Polyommatus*, *Lysandra*, *Neolysandra*, *Aricia*, *Glabroculus* and *Alpherakya*, but differs from them in the narrow uncus and hairless eyes. The aedeagus in *Eumedonia* is comparatively slender and more pointed, resembling that in *Agriades* (Zhdanko, 2004), yet the wing patterns are very different between *Eumedonia* and *Agriades*.

The genus Cyaniris. The genus *Cyaniris* (TS: *Zephyrus argianus* Dalman, 1816, now regarded as a synonym of *Papilio semiargus* Rottemburg, 1775) is often considered to be close to *Polyommatus* s.s. (Hesselbarth et al., 1995; Bálint and Johnson, 1997), but this relationship was questioned on the basis of morphological (Zhdanko, 2004) and molecular analyses (Wiemers et al., 2010). Indeed, our data indicate that *Cyaniris* is not closely related to *Polyommatus* s.s. Instead, it forms a clade together with *Rimisia* and *Agriades sensu lato*, although the support for this relationship is not high. The age of divergence of the *Cyaniris* lineage (4.4 Myr) is sufficient to maintain it as an independent genus.

Cyaniris differs from *Polyommatus*, *Lysandra*, *Neolysandra*, *Aricia*, *Glabroculus*, *Alpherakya* and *Plebejidea* in having a narrow, nearly pointed uncus. It differs from other taxa that also have narrow uncus in the presence of hairs densely covering the eyes and by having a longer aedeagus (Zhdanko, 2004). Additionally, representatives of the genus have no marginal and submarginal pattern on the wing underside. The combination of these characters is characteristic for the genus *Cyaniris*.

The genus Rimisia. The monotypic Central Asian genus *Rimisia* (TS: *Lycaena miris* Staudinger, 1881) has been considered to be close to *Glabroculus* (Bálint and Johnson, 1997; Tuzov et al., 2000), with which it shares a similar pattern on the underside of the wings. This hypothesis is not supported by our data, since *Rimisia* is recovered as sister to *Agriades* with a divergence of more than 4 Myr. The genus *Rimisia* displays an unusual combination of morphological characters: valvae in the male genitalia similar to those of the species *Polyommatus icarus*, short and S-shaped aedeagus, naked eyes and peculiar female genitalia with small papillae anales (Zhdanko, 2004). *Rimisia miris* is considered to have no metallic marginal spots on the hind wings (Zhdanko, 2004), but our analysis of the morphology revealed that the species is variable with respect to this character and some specimens bear metallic scales on the marginal spots.

Agriades clade. According to our results, the genus *Agriades* (TS: *Papilio glandon* Prunner, 1798) originated 4.2 Mya and includes three monophyletic lineages that may be considered as subgenera: *Albulina* (*orbitulus*) (originated 3.6 Mya), *Vacciniina* s.s. (*optilete*) and *Agriades* s.s. (*glandon*, *pheretiades*, *podarce* and *pyrenaicus*) (the latter two split 3.2 Mya). These three taxa are often considered to be distinct genera (e.g. Higgins, 1975), and they indeed differ in their wing patterns (Fig. 5) and larval food plants (Table 3). The close relationship between *Albulina* and *Vacciniina* was recognized by Bálint and Johnson (1997). Our analysis strongly supports the grouping of *Agriades* s.s., *Albulina* and *Vacciniina* s.s. Within this group, *Agriades* s.s. and *Vacciniina* s.s. are sister taxa and *Albulina* is sister to the rest. As our study resulted in the fusion of the taxa *Agriades* s.s., *Albulina* and *Vacciniina* s.s in one genus, the following new combinations result: *Agriades optilete* **comb. nov,** *Agriades orbitulus* **comb. nov.**

Lysandra + (*Neolysandra* + *Polyommatus*) clade. This clade is recovered with a high support in our analysis, and it is estimated to have diverged ca. 5.7 Mya. Within this clade, three genera—*Lysandra*, *Neolysandra* and *Polyommatus*—are recognized in accordance with the criteria discussed above.

Lysandra clade. The genus *Lysandra* (TS: *Papilio coridon* Poda, 1761) is monophyletic and sister to the clade *Neolysandra* + *Polyommatus* with good support. The most characteristic morphological feature of the genus is the clearly chequered wing fringes. This character is not exclusive within the subtribe Polyommatina, and it is found in the distantly related genera *Alpherakya*, *Maurus* and *Grumiana*, as well as in some genera of the Neotropical clade. The hypothesis that *Lysandra* is a synonym of *Meleageria* (which includes the species *daphnis* and *marcida*) (Hesselbarth et al., 1995) is not supported by our phylogeny (see also Wiemers et al., 2010).

Neolysandra clade. In our analysis, the genus *Neolysandra* (TS: *Lycaena diana* Miller, 1912) emerges as a well supported lineage that is a sister to *Polyommatus*. Morphologically *Neolysandra* differs from other genera by the markedly wide and elliptical uncus. Moreover, it differs from the most similar genera *Lysandra* and *Polyommatus* in having short and scarce hairs covering the eyes and in displaying a reduced marginal and submarginal pattern on the wing underside (Zhdanko, 2004). In the molecular reconstruction made by Wiemers et al. (2010), *Neolysandra* was recovered as a polyphyletic taxon. Several reasons might explain this: the taxon sampling (the type species *N. diana* was not included), lack of resolution (the phylogeny was based on two relatively short sequences), and incomplete outgroup sampling (only the phylogenetically distant taxa *Cyaniris semiargus* and *Freyeria trochilus* were used to root the tree). What we consider *Neolysandra* (including the taxa *diana* and *coelestina*) corresponds to Wiemers' *Neolysandra* group I.

Polyommatus clade. In our analysis, the genus *Polyommatus* (TS: *Papilio icarus* Rottemburg, 1775) emerged as a distinct lineage about 4.3 Mya. It is composed of taxa sometimes included in the genera/subgenera *Actisia* Koçak & Kemal, 2001 (TS: *Lycaena actis* Herrich-Schäffer, 1851—a junior synonym, the valid synonym is *Lycaena atys* (Gerhard, 1851); *Admetusia* Koçak & Seven, 1998 (TS: *Papilio admetus* Esper, 1783); *Agrodiaetus* Hübner, 1822

Fig. 5. Representative taxa of the genus *Agriades*. Similarly to other species-rich genera in the subtribe Polyommatina, despite their monophyly and genetic similarities, the genus *Agriades* is morphologically quite diverse with respect to both wing upper side and underside colours and patterns. (a,b) *Agriades orbitulus*; (c,d) *Agriades glandon*; (e,f) *Agriades pheretiades*; (g,h) *Agriades pyrenaicus*; (i,j) *Agriades podarce*; (k,l) *Agriades optilete*.

(= *Hirsutina* Tutt, [1909]) (TS: *Papilio damon* Denis & Schiffermüller, 1775); *Antidolus* Koçak & Kemal, 2001 (TS: *Papilio dolus* var. *antidolus* Rebel, 1901); *Bryna* Evans, 1912 (TS: *Lycaena stoliczkana* Felder & Felder, 1865); *Damaia* Koçak & Kemal, 2001 (TS: *Lycaena dama* Staudinger, 1892); *Meleageria* De Sagarra, 1925 (TS: *Papilio daphnis* Esper, 1778); *Musa* Koçak & Kemal, 2001 (TS: *Polyommatus musa* Koçak & Hosseinpour, 1996); *Paragrodiaetus* Rose & Schurian, 1977 (TS: *Lycaena glaucias* Lederer, 1870); *Peileia* Koçak & Kemal, 2001 (TS: *Polyommatus peilei* Bethune-Baker, 1921); *Phyllisia* Koçak & Kemal, 2001 (TS: *Papilio damon* var. *phyllis* Christoph, 1877); *Plebicula* Higgins, 1969 (TS: *Papilio argester* Bergträsser, 1779); *Polyommatus* Latreille, 1804 (TS: *Papilio icarus* Rottemburg, 1775); *Sublysandra* Koçak, 1977 (TS: *Lycaena candalus* Herrich-Schäffer, 1851); *Thersitesia* Koçak & Seven, 1998 (TS: *Lycaena thersites* Cantener, 1834); *Transcaspius* Koçak & Kemal, 2001 (TS: *Lycaena kindermanni* var. *transcaspica* Heyne, 1895); and *Xerxesia* Koçak & Kemal, 2001 (TS: *Lycaena damone* var. *xerxes* Staudinger, 1899). Several of these taxa are recovered as monophyletic, but no subclade is older than 4 Myr. Thus, according to our criteria, they should not be treated as genera. The composition and relationships obtained are notably similar to those obtained by Zhdanko (2004) based on a morphological analysis (e.g. *Lysandra* and *Neolysandra* are separate genera), but differ in some details (e.g. in the position of *Agrodiaetus*). Wiemers et al. (2010) specifically addressed relationships in this genus based on molecular data from two genetic markers and a different set of outgroup taxa. Deeper relationships are frequently not supported in their study and do not always match those obtained here. The most characteristic morphological features of the genus are the marked downward expansion of the ventral margin of the uncus and the presence of all the basic elements of the wing pattern (Zhdanko, 2004). *Polyommatus* differs from *Lysandra* in having white or grey (not chequered) fringes. It differs from *Neolysandra* in the presence of long hairs densely covering the eyes.

One of the subclades in our analysis is formed by the taxa traditionally included in *Agrodiaetus* (*P. damocles*, *P. ripartii*, *P. surakovi* and *P. damon*) and *Paragrodiaetus* (*P. glaucias* and *P. erschoffii*), thus our results confirm previous results showing that *Agrodiaetus* is a monophyletic entity that includes *Paragrodiaetus* (Kandul et al., 2004, 2007; Wiemers et al., 2010). Morphologically, the subgenus *Agrodiaetus* differs from other genera and subgenera of the subtribe Polyommatina in two autapomorphic characters of the male genitalia: distal extremity of aedeagus pronouncedly swollen (Zhdanko, 1983) and uncus markedly constricted dorsoventrally (Zhdanko, 2004). Our data also strongly support that the taxon *P. stempfferi* is sister to the *Agrodiaetus* clade, and that *P. escheri* is sister to the *P. stempfferi* + *Agrodiaetus* clade. The taxa *P. myrrha* and *P. cornelia*, representative of the taxon *Sublysandra*, form another subgroup of *Polyommatus* that is recovered with low support and with unresolved position. *Sublysandra* is usually considered to be a subgenus of *Polyommatus* (Bálint and Johnson, 1997; Zhdanko, 2004; Wiemers et al., 2010) and is morphologically similar to *Polyommatus* s.s. The subclade representing *Meleageria* (*P. daphnis* and *P. marcida*) is recovered with good support as sister to the species *P. amandus*. The close relationship between *P. amandus* and *P. daphnis* + *P. marcida* is surprising and has not been proposed previously.

The last supported subclade is formed by *Polyommatus* s.s. + (*Plebicula* + *Thersitesia*). The sister relationship of the taxa representing *Plebicula* (*P. dorylas* and *P. nivescesns*) and *Thersitesia* (*P. thersites*) was first recovered by Wiemers et al. (2010). *Polyommatus* s.s. was recovered as monophyletic with high support. Within this clade, the Central Asian species *P. hunza* and *P. venus* (which sometimes have been placed together in the genus *Bryna*) form a clade that is sister to the rest (*erotides* and *icarus*). This Central Asian subclade was also recovered by Wiemers et al. (2010).

Conclusion

A multilocus molecular phylogeny has clarified relationships within the Polyommatina, and molecular age estimates have helped to establish criteria specific for the higher-level taxonomy of this group. Each of the resulting clades that we designate to be a genus displays a distinguishing combination of morphological characters, but most of these characters are not unique to a single genus. The high evolutionary lability of many morphological characters traditionally used to infer relationships in this lineage of butterflies (metallic spots in the hind wing underside, blue versus brown male wing colour, shape of the valvae, membranous ventral fold in the inner part of valvae, marked discal spot on the fore wing upper side, number of segments in the antennal club, pilosity in the eyes, presence of small tails in the hind wing, etc.) is apparent, and explains why the taxonomy of the Polyommatina has been so controversial. Based on our phylogenetic results and the criteria outlined above, we propose the following systematic arrangement for the subtribe Polyommatina (in parentheses we list objective and subjective synonyms for the generic names, objective synonyms are indicated by the sign "="; in brackets we provide a tentative list of species for each genus in alphabetical order; likely synonyms for species are not included; species that were analysed in this study are highlighted in bold):

Subtribe **Polyommatina** *Swainson, 1827*

Genus ***Polyommatus*** Latreille, 1804 (*Actisia* Koçak & Kemal, 2001; *Admetusia* Koçak & Seven, 1998; *Agrodiaetus* Hübner, 1822 (= *Hirsutina* Tutt, [1909]); *Antidolus* Koçak & Kemal, 2001; *Bryna* Evans, 1912; *Dagmara* Koçak & Kemal, 2001; *Damaia* Koçak & Kemal, 2001; *Juldus* Koçak & Kemal, 2001; *Meleageria* De Sagarra, 1925; *Musa* Koçak & Kemal, 2001; *Paragrodiaetus* Rose & Schurian, 1977; *Peileia* Koçak & Kemal, 2001; *Phyllisia* Koçak & Kemal, 2001; *Plebicula* Higgins, 1969; *Sublysandra* Koçak, 1977; *Thersitesia* Koçak & Seven, 1998; *Transcaspius* Koçak & Kemal, 2001; *Xerxesia* Koçak & Kemal, 2001) [*P. abdon* Aistleitner & Aistleitner, 1994), *P. achaemenes* Skala, 2002, *P. actinides* (Staudinger, 1886), *P. admetus* (Esper, 1783), *P. aedon* (Christoph, 1877), *P. aereus* Eckweiler, 1998, *P. afghanicus* (Forster, 1973), *P. ahmadi* (Carbonell, 2001), *P. alcestis* Zerny, 1932, *P. aloisi* Bálint, 1998, *P. altivagans* (Forster, 1956), ***P. amandus* (Schneider, 1792)**, *P. amor* (Lang, 1884), *P. annamaria* Bálint, 1992, *P. anticarmon* (Koçak, 1983), *P. antidolus* (Rebel, 1901), *P. arasbarani* (Carbonell & Naderi, 2000), *P. ardschira* (Brandt, 1938), *P. ariana* (Moore, 1865), *P. aroaniensis* (Brown, 1976), *P. artvinensis* (Carbonell, 1997), *P. aserbeidschanus* (Forster, 1956), *P. atlanticus* (Elwes, 1906), *P. attalaensis* Carbonell, Borie & De Prins, 2004, *P. atys* (Gerhard, 1851), *P. avinovi* *Sthchetkin*, 1980, *P. baltazardi* (de Lesse, 1963), *P. baytopi* (de Lesse, 1959), *P. belovi* (Dantchenko & Lukhtanov, 2005), *P. bilgini* (Lukhtanov and Dantchenko, 2002), *P. bilucha* (Moore, 1884), *P. birunii* Eckweiler & 10 Hagen, 1998, *P. bogra* Evans, 1932, *P. boisduvalii* (Herrich-Schäffer, 1843), *P. bollandi* Dumont, 1998, *P. buzulmavi* Carbonell, 1991, *P. caeruleus*

(Staudinger, 1871), *P. carmon* (Herrich-Schäffer, 1851, *P. celina* (Austaut, 1879), *P. charmeuxi* (Pagès, 1994), *P. cilicius* (Carbonell, 1998), *P. ciloicus* de Freina & Witt, 1983, **P. cornelia** (**Fryer, 1851**), *P. cyaneus* (Staudinger, 1899), *P. dagestanicus* (Forster, 1960), *P. dagmara* (Grum-Grshimaïlo, 1888), *P. dama* (Staudinger, 1992), ***P. damocles*** (**Herrich-Schäffer, 1844**), ***P. damon*** (**Denis & Schiffermüller, 1775**), *P. damone* (Eversmann, 1841), *P. damonides* (Staudinger, 1899), *P. dantchenkoi* (Lukhtanov & Wiemers, 2003), ***P. daphnis*** (**Denis & Schiffermüller, 1775**), *P. deebi* (Larsen, 1974), *P. demavendi* (Pfeiffer, 1938), *P. dizinensis* (Schurian, 1982), *P. dolus* (Hübner, 1823), ***P. dorylas*** (**Denis & Schiffermüller, 1775**), *P. drunela* Swinhoe, 1910, *P. eckweileri* 10 Hagen, 1988, *P. ectabanensis* (de Lesse, 1964), *P. elbursicus* (Forster, 1956), *P. eleniae* Coutsis & De Prins, 2005, *P. erigone* (Grum-Grshimaïlo, 1890), *P. eriwanensis* (Forster, 1960), *P. ernesti* (Eckweiler, 1989), *P. eroides* (Frivaldszky, 1835), *P. eros* (Ochsenheimer, 1808), ***P. erotides*** (**Staudinger, 1892**), ***P. erschoffii*** (**Lederer, 1869**), ***P. escheri*** (**Hübner, 1823**), *P. fabressei* (Oberthür, 1910), *P. faramarzi* Skala, 2001, *P. femininoides* (Eckweiler, 1987), *P. firdussii* (Forster, 1956), *P. florenciae* (Tytler, 1926), *P. forresti* Bálint, 1992, *P. frauvartianae* Bálint, 1997, *P. fulgens* (de Sagarra, 1925), ***P. glaucias*** (**Lederer, 1870**), *P. golgus* (Hübner, 1813), *P. guezelmavi* Olivier, Puplesiene, van der Poorten, De Prins & Wiemers, 1999, *P. haigi* (Lukhtanov and Dantchenko, 2002), *P. hamadanensis* (de Lesse, 1959), *P. hopfferi* (Herrich-Schäffer, 1851), *P. huberti* (Carbonell, 1993), *P. humedasae* (Toso & Balletto, 1976), ***P. hunza*** (**Grum-Grshimaïlo, 1890**), *P. icadius* (**Grum-Grshimaïlo, 1890**), ***P. icarus*** (**Rottemburg, 1775**), *P. interjectus* (de Lesse, 1960), *P. iphicarmon* Eckweiler & Rose, 1993, *P. iphidamon* (Staudinger, 1899), *P. iphigenia* (Herrich-Schäffer, 1847), *P. iphigenides* (Staudinger, 1886), *P. isauricoides* Graves, 1923, *P. ishkashimicus* Shchetkin, 1986, *P. juldusus* (Staudinger, 1886), *P. kamtshadalis* (Sheljuzhko, 1933), *P. karacetinae* (Lukhtanov and Dantchenko, 2002), *P. karatavicus* (Lukhtanov, 1990), *P. karindus* (Riley, 1921), *P. kendevani* (Forster, 1956), *P. khorasanensis* (Carbonell, 2001), *P. klausschuriani* 10 Hagen, 1999, *P. kurdistanicus* (Forster, 1961), *P. lama* (Grum-Grshimaïlo, 1891), *P. larseni* (Carbonell, 1994), *P. lukhtanovi* (Dantchenko, 2005), *P. luna* Eckweiler, 2002, *P. lycius* (Carbonell, 1996), *P. magnificus (Grum-Grshimaïlo, 1885)*, *P. maraschi* (Forster, 1956), ***P. marcida*** (**Lederer, 1870**), *P. masulensis* 10 Hagen & Schurian, 2000, *P. mediator* (Dantchenko & Churkin, 2003), *P. melanius* (Staudinger, 1886), *P. menalcas* (Freyer, 1837), *P. menelaos* Brown, 1976, *P. meoticus* Zhdanko & Shchurov, 1998, *P. merhaba* De Prins, van der Poorten, Borie, van Oorschot, Riemis & Coenen, 1991, *P. mithridates* (Staudinger, 1878), *P. mofidii* (de Lesse, 1963), *P. morgani* (Le Cerf, 1909), *P. muellerae* Eckweiler, 1997, *P. muetingi* (Bálint, 1992), *P. musa* Koçak & Hosseinpour, 1996, ***P. myrrha*** (**Herrich-Schäffer, 1851**), *P. nephohiptamenos* (Brown & Coutsis, 1978), *P. nepalensis* Forster, 1961, *P. ninae* (Forster, 1956), ***P. nivescens*** (**Keferstein, 1851**), *P. nuksani* (Forster, 1937), *P. orphicus* (Kolev, 2005), *P. paulae* Wiemers & De Prins, 2004, *P. peilei* Bethune-Baker. 1921, *P. pfeifferi* (Brandt, 1938), *P. phyllides* (Staudinger, 1986), *P. phyllis* (Christoph, 1877), *P. pierceae* (Lukhtanov and Dantchenko, 2002), *P. pierinoi* Bálint, 1995, *P. poseidon* (Herrich-Schäffer, 1851), *P. poseidonides* (Staudinger, 1886), *P. posthumus* Christoph, 1877), *P. pseuderos* (Moore, 1879), *P. pulchella (Bernardi, 1951)*, *P. putnami* (Lukhtanov and Dantchenko, 2002), ***P. ripartii*** (**Freyer, 1830**), *P. rjabovianus* (Koçak, 1980), *P. rovshani* (Dantchenko & Lukhtanov, 1994), *P. schuriani* (Rose, 1978), *P. sennanensis* (de Lesse, 1959), *P. sertavulensis* (Koçak, 1979), *P. shahkuhensis* (Lukhtanov & Shapoval, 2008), *P. shahrami* (Skala, 2001), *P. shamil* (Dantchenko, 2000), *P. shirkuhensis* 10 Hagen & Eckweiler, 2001, *P. sigberti* Olivier, van der Poorten, Puplesiene & De Prins, 2000, *P. sorkhensis* Eckweiler, 2003, ***P. stempfferi*** (**Brand, 1938**), *P. stigmatifera* (Courvoisier, 1903), ***P. surakovi*** (**Dantchenko & Lukhtanov, 1994**), *P. tankeri* (de Lesse, 1960), *P. tenhageni* Schurian & Eckweiler, 1999, *P. theresiae* Schurian, van Oorschot & van den Brink, 1992, ***P. thersites*** (**Cantener, 1834**), *P. transcaspicus* (Heyne, 1895), *P. tshetverikovi* Nekrutenko, 1977, *P. tsvetajevi (Kurentzov, 1970)*, *P. turcicolus* (Koçak, 1977), *P. turcicus* (Koçak, 1977), *P. urmiaensis* (Schurian & 10 Hagen, 2003), *P. valiabadi* (Rose & Schurian, 1977), *P. vanensis* (de Lesse, 1958), *P. vaspurakani* (Lukhtanov & Dantchenko, 2003), ***P. venus*** (**Staudinger, 1886**), *P. violetae* (Gómez-Bustillo, Expósito & Martínez, 1979), *P. vagneri* (Forster, 1956), *P. wiskotti* (Courvoisier, 1910), *P. yurinekrutenko* Koçak, 1996, *P. zapvadi* (Carbonell, 1993), *P. zarathustra* Eckweiler, 1997, *P. zardensis* Schurian & 10 Hagen, 2001]

Genus ***Neolysandra*** Koçak, 1977 [***N. coelestina*** (**Eversmann, 1843**), *N. corona* (Verity, 1936), ***N. diana*** (**Miller, 1913**), *N. ellisoni* (Pfeiffer, 1931), *N. fatima* Eckweiler & Schurian, 1980, *N. fereiduna* Skala, 2002].

Genus ***Lysandra*** Hemming, 1933 [(= *Uranops* Hemming, 1929); (= *Argus* Scopoli, 1763)] [*L. albicans* (Gerhard, 1851), *L. arzanovi* (Stradomsky & Shchurov, 2005, ***L. bellargus*** (**Rottemburg, 1775**), *L. caelestissima* (Verity, 1921), ***L. coridon*** (**Poda, 1761**), *L. corydonius* (Herrich-Schäffer, 1852), *L. dezina* de Freina & Witt, 1983, *L. gennargenti* Leigheb, 1987, *L. hispana* (Herrich-Schäffer, 1851), *L. melamarina* Dantchenko, 2000, *L. nufrellensis* Schurian, 1977, *L. ossmar* (Gerhard, 1851), ***L. punctifera*** (**Oberthür, 1876**), *L. sheikh* Dantchenko, 2000, *L. syriaca* Tutt, 1910].

Genus ***Agriades*** Hübner, [1819] ((= *Latiorina* Tutt, [1909]); *Albulina* Tutt, 1909; *Himalaya* Koçak &

Seven, 1998; *Mestore* Koçak & Kemal, 2007; *Vacciniina* Tutt, 1909; *Xinjiangia* Huang & Murayama, 1988) [*A. amphirrhoe* (Oberthür, 1910), *A. arcaseia* (Fruhstorfer, 1916), *A. asiatica* (Elwes, 1882), *A. cassiope* Emmel & Emmel, 1998, *A. dis* (Grum-Grshimaïlo, 1891), ***A. glandon*** (**de Prunner, 1798**), *A. jaloka* (Moore, 1875), *A. janigena* (Riley, 1923), *A. kumukuleensis* (Huang & Murayama, 1988), *A. kurtjohnsoni* Bálint, 1997, *A. lehanus* (Moore, 1878), *A. luana* (Evans, 1915), *A. morsheadi* (Evans, 1923), ***A. optilete*** (**Knoch, 1781**), ***A. orbitulus*** (**de Prunner, 1798**), ***A. pheretiades*** (**Eversmann, 1843**), ***A. podarce*** (**Felder & Felder,1865**), ***A. pyrenaicus*** (**Boisduval, 1840**), *A. sikkima* (Moore, 1884)].

Genus ***Rimisia*** Zhdanko, 1994 [***R. miris*** (**Staudinger, 1881**)].

Genus ***Cyaniris*** Dalman, 1816 ((= *Nomiades* Hübner, [1819]); *Glaucolinea* Wang & Rehn, 1999) [*C. bellis* (Freyer, 1842), ***C. semiargus*** (**Rottemburg, 1775**)].

Genus ***Eumedonia*** Forster, 1938 [***E. eumedon*** (**Esper, 1780**), *E. kogistana* (Grum-Grshimaïlo, 1888), ***E. persephatta*** (**Alphéraky, 1881**)].

Genus ***Plebejidea*** Koçak, 1983 [*P. afshar* (Eckweiler, 1998), ***P. loewii*** (**Zeller, 1847**)].

Genus ***Maurus*** Bálint, [1992] [***M. vogelii*** (**Oberthür, 1920**)].

Genus ***Kretania*** Beuret, 1959 (*Plebejides* Sauter, 1868) [***K. alcedo*** (**Christoph, 1877**), *K. allardi* (Oberthür, 1874), *K. beani* (Bálint and Johnson, 1997), *K. csomai* (Bálint, 1992), ***K. eurypilus*** (**Freyer, 1851**), *K. hesperica* (Rambur, 1839), *K. iranica* (Forster, 1938), *K. martini* (Allard, 1867), *K. nicholli* (Elwes, 1901), *K. patriarcha* (Bálint, 1992), *K. philbyi* (Graves, 1925), *K. psylorita* (Freyer, 1845), ***K. pylaon*** (**Fischer von Waldheim, 1832**), *K. sephirus* (Frivaldszky, 1835), *K. trappi* (Verity, 1927), *K. usbeka* (Forster, 1939), ***K. zephyrinus*** (**Christoph, 1884**)].

Genus ***Afarsia*** Korb and Bolshakov, 2011 (= *Farsia* Zhdanko, 1992) [*A. antoninae* (Lukhtanov, 1999), *A. ashretha* (Evans, 1925), *A. hanna* (Evans, 1932), *A. iris* (Lang, 1884), *A. jurii* (Tshikolovets, 1997), ***A. morgiana*** *(*(**Kirby, 1871**), *A. omotoi* (Forster, 1972), *A. rutilans* (Staudinger, 1886), *A. sieversii* (Christoph, 1873)].

Genus ***Aricia*** Reichenbach, 1817 ((= *Gynomorphia* Verity, 1929); *Pseudoaricia* Beuret, 1959; *Ultraaricia* Beuret, 1959; *Umpria* Zhdanko, 1994) [***A. agestis*** (**Denis & Schiffermüller, 1775**), *A. anteros* (Freyer, 1838), ***A. artaxerxes*** (**Fabricius, 1793**), *A. bassoni* (Larsen, 1974), ***A. chinensis*** (**Murray, 1874**), *A. cramera* (Eschscholtz, 1821), ***A. crassipuncta*** (**Christoph, 1893**), *A. hyacinthus* (Herrich-Schäffer, 1847), *A. isaurica* (Staudinger, 1871), *A. montensis* (Verity, 1928), *A. morronensis* (Ribbe, 1910), ***A. nicias*** (**Meigen, 1829**), *A. teberdina* (Sheljuzhko, 1934), *A. torulensis* (Hesselbarth & Siepe, 1993), ***A. vandarbani*** (**Pfeiffer, 1937**)].

Genus ***Glabroculus*** Lvovsky, 1993 (*Elviria* Zhdanko, 1994) [***G. cyane*** (**Eversmann, 1837**), ***G. elvira*** (**Eversmann, 1854**).

Genus ***Alpherakya*** Zhdanko, 1994 [*A. bellona* (Grum-Grshimaïlo, 1888), *A. devanica* (Moore, 1875), *A. pilgram* (Bálint and Johnson, 1997), ***A. sarta*** (**Alphéraky, 1881**), *A. sartoides* (Swinhoe, 1910)].

Genus ***Plebejus*** Kluk, 1780 ((= *Rusticus* Hübner, [1806]); (= *Lycoena* Nicholl, 1901); *Lycaeides* Hübner, [1919]) [*P. aegina* (Grum-Grshimaïlo, 1891), *P. agnatus* (Staudinger, 1889), ***P. anna*** (**Edwards, 1861**), *P. argiva* (Staudinger, 1886), ***P. argus*** (**Linnaeus, 1758**), ***P. argyrognomon*** (**Bergsträsser, 1779**), *P. bergi* (Kusnezov, 1908), *P. caspicus* (Forster, 1936), *P. choltagi* (Zhdanko & Churkin, 2001), *P. christophi* (Staudinger, 1874), *P. cleobis* (Bremer, 1861), *P. dzhizaki* Zhdanko, 2000, *P. eversmanni* (Lang, 1884), *P. fridayi* Chermock, 1945, *P. fyodor* Hsu, Bálint & Johnson, 2000, *P. ganssuensis* (Grum-Grshimaïlo, 1891), ***P. idas*** (**Linnaeus, 1760**), *P. kwaja* (Evans, 1932), *P. lepidus* Zhdanko, 2000, *P. maidantagi* Zhdanko & Churkin, 2001, *P. maracandicus* (Erschoff, 1874), ***P. melissa*** (**Edwards, 1873**), *P. mongolicus* (Rühl, 1893), *P. noah* (Herz, 1900), *P. nushibi* Zhdanko, 2000, *P. planorum* (Alphéraky, 1881), *P. pseudaegon* (Butler, 1882), *P. qinghaiensis* (Murayama, 1992), *P. rogneda* (Grum-Grshimaïlo, 1990), *P. roxane* (Grum-Grshimaïlo, 1887), *P. samudra* (Moore, 1875), *P. samuelis* (Nabokov, 1844), *P. shuroabadicus* (Sthchetkin, 1963), *P. sinicus* (Forster, 1936), *P. subsolanus* (Eversmann, 1851), *P. tancrei* (Graeser, 1888), *P. tillo* Zhdanko & Churkin, 2001, *P. tomyris* (Grum-Grshimaïlo, 1890), *P. transcaucasicus* (Rebel, 1901), *P. uiguricus* Zhdanko, 2000].

Genus ***Pamiria*** Zhdanko, 1994 [***P. chrysopis*** (**Grum-Grshimaïlo, 1888**), *P. galathea* (Blanchard, 1844), *P. issa* (Zhdanko, 1992), *P. margo* Zhdanko, 2002, *P. metallica* (Felder & Felder, 1865), *P. omphisa* (Moore, 1875), *P. selma* (Koçak, 1996)].

Genus ***Patricius*** Bálint, [1992] (*Themisia* Zhdanko, 2002) [*P. felicis* (Oberthür, 1886), ***P. lucifer*** (**Staudinger, 1866**), *P. lucifugus* (Fruhstorfer, 1915), *P. lucina* (Grum-Grshimaïlo, 1902), *P. sagona Zhdanko*, 2002, *P. themis* (Grum-Grshimaïlo, 1891), *P. younghusbandi* (Elwes, 1906)].

Genus *Grumiana* Zhdanko, 2004 [*G. berezowskii* (Grum-Grshimaïlo, 1902) (not studied by us, morphologically close to *Plebejus* (Zhdanko, 2004)].

Genus ***Rueckbeilia*** gen. nov. [***R. fergana*** (**Staudinger, 1881**), *R. rosei* (Eckweiler, 1989)].

Genus ***Icaricia*** Nabokov, [1945] [***I. acmon*** (**Westwood, 1851**), *I. cotundra* Scott & Fisher, 2006, ***I. icarioides*** (**Boisduval, 1852**), *I. lupini* (Boisduval, 1869), *I. neurona* (Skinner, 1902), ***I. saepiolus*** (**Boisduval, 1852**), ***I. shasta*** (**Edwards, 1862**)].

Genus ***Plebulina*** Nabokov, [1945] [***P. emigdionis*** (**Grinnell, 1905**)].

Genus ***Freyeria*** Courvoisier, 1920 [*F. minuscule* (Aurivillius, 1909), ***F. putli* (Kollar, 1844), *F. trochylus* (Freyer, 1844)**].

Genus ***Luthrodes*** Druce, 1895 (*Edales* Swinhoe, [1910]; *Lachides* Nekrutenko, 1984) [*L. boopis* (Fruhstorfer, 1897), *L. buruana* (Holland, 1900), ***L. cleotas* (Guérin-Méneville, 1831)**, *L. contracta* (Butler, 1880), *L. ella* (Butler, 1881), ***L. galba* (Lederer, 1855)**, *L. mindora* (Felder & Felder, 1865), ***L. pandava* (Horsfield, 1829)**, *L. peripatria* (Hsu, 1989)].

Genus ***Chilades*** Moore, [1881] [*C. alberta* (Butler, 1901), *C. eleusis* (Demaison, 1888), *C. elicola* (Strand, 1911), *C. kedonga* (Grose-Smith, 1898), ***C. lajus* (Stoll, 1780)**, *C. naidina* (Butler, 1886), *C. parrhasius* (Fabricius, 1793), *C. sanctithomae* (Sharpe, 1893), *C. serrula* (Mabille, 1890)]. Species incertae sedis: *C. roemli* Kalis, 1933, *C. saga* (Grose-Smith, 1895), *C. yunnanensis* Watkins, 1927.

Genus ***Itylos*** Draudt, 1921 ((= *Ithylos* Forster, 1955); *Ityloides* Balletto, 1993; *Madeleinea* Bálint, 1993 (= *Nivalis* Balletto, 1993); *Parachilades* Nabokov, 1945) [*I. ardisensis* (Bálint & Lamas, 1997), *I. bella* (Bálint & Lamas, 1997), *I. cobaltana* (Bálint & Lamas, 1994), *I. colca* (Bálint & Lamas, 1997), *I. fumosus* (Balletto, 1993), *I. gradoslamasi* (Bálint, 1997), ***I. huascarana* (Bálint & Lamas, 1994), *I. koa* (Druce, 1876**), *I. lea* (Benyamini, Bálint and Johnson, 1995), *I. lolita* (Bálint, 1993), *I. ludicra* (Weymer, 1890), *I. malvasa* (Bálint & Pyrcz, 2000), ***I. mashenka* (Bálint, 1993)**, *I. mira* Bálint & Lamas, 1999, *I. moza* (Staudinger, 1894), *I. nodo* (Bálint and Johnson, 1995), *I. pacis* Draudt, 1921, *I. pasco* Bálint & Lamas, 1994, *I. pelorias* (Weymer, 1890), *I. pnin* Bálint, 1993, ***I. sigal* (Benyamini, Bálint and Johnson, 1995)**, ***I. tintarrona* (Bálint and Johnson, 1995)**, ***I. titicaca* (Weymer, 1890)**, *I. vokoban* (Bálint and Johnson, 1995)].

Genus ***Paralycaeides*** Nabokov, 1945 (*Boliviella* Balletto, 1993) [***P. inconspicua* (Draudt, 1921)**, *P. shade* Bálint, 1993, ***P. vapa* (Staudinger, 1894)**].

Genus ***Pseudolucia*** Nabokov, 1945 ((= *Pallidula* Balletto, 1993); *Cherchiella* Balletto, 1993; *Facula* Balletto, 1992) [*P. andina* (Bartlett-Calvert, 1893), *P. annamaria* Bálint & Johnson, 1993, *P. arauco* Bálint, Benyamini & Johnson, 2001, *P. argentina* (Balletto, 1993), ***P. asafi* Benyamini, Bálint and Johnson, 1995**; *P. aureliana* Bálint & Johnson, 1993, *P. avishai* Benyamini, Bálint and Johnson, 1995; *P. barrigai* Benyamini & Bálint, 2011, *P. benyamini* Bálint and Johnson, 1995; ***P. charlotte* Bálint and Johnson, 1995**; ***P. chilensis* (Blanchard, 1852)**, *P. clarea* Bálint & Johnson, 1993, *P. collina* (Philippi, 1859), *P. dubi* Bálint, 2001, *P. faundezi* Benyamini & Bálint, 2011, *P. grata* (Köhler, 1934), *P. hazearum* Bálint & Johnson, 1993, *P. henyah* Bálint, Benyamini & Johnson, 2001, *P. humbert* Bálint and Johnson, 1995; *P. johnsoni* Benyamini & Bálint, 2011, *P. jujuyensis* Bálint, Eisele & Johnson, 2000, *P. kechico* Bálint, Benyamini & Johnson, 2001, *P. kinbote* Bálint & Johnson, 1993, *P. lanin* (Bálint & Johnson, 1993), *P. luzmaria* Benyamini & Bálint, 2011, *P. magellana* Benyamini, Bálint and Johnson, 1995; *P. munozae* Benyamini & Bálint, 2011, *P. neuqueniensis* Bálint and Johnson, 1995; *P. oligocyaena* (Ureta, 1956), *P. oraria* Bálint & Benyamini, 2001, *P. parana* Bálint, 1993, *P. patago* (Mabille, 1889), *P. penai* (Bálint & Johnson, 1993), *P. plumbea* (Butler, 1881), *P. scintilla* (Balletto, 1993), *P. shapiroi* Bálint and Johnson, 1995; ***P. sibylla* (Kirby, 1871)**, *P. sigal* Benyamini & Bálint, 2011, *P. talia* Bálint, Benyamini & Johnson, 1995, *P. tamara* Bálint and Johnson, 1995; *P. ugartei* Bálint & Benyamini, 2001, *P. valentina* Benyamini & Bálint, 2011, ***P. vera* Bálint & Johnson, 1993**, *P. whitakeri* Bálint and Johnson, 1995; *P. zina* Benyamini, Bálint and Johnson, 1995, *P. zoellneri* Benyamini & Bálint, 2011].

Genus ***Nabokovia*** Hemming, 1960 (= *Pseudothecla* Nabokov, 1945) [*N. ada* Bálint and Johnson, 1994, ***N. cuzquenha* Bálint & Lamas, 1997**, ***N. faga* (Dognin, 1895)**].

Genus ***Eldoradina*** Balletto, 1993 (= *Polytheclus* Bálint & Johnson, 1993) [***E. cyanea* (Balletto, 1993)**, *E. sylphis* Draudt, 1921].

Genus ***Hemiargus*** Hübner, 1818 [***H. huntingtoni* Rindge & Comstock, 1953**, ***H. martha* (Dognin, 1887)**, ***H. hanno* (Stoll, 1790)***, ***H. ramon* (Dognin, 1887)**].

Genus ***Echinargus*** Nabokov, 1945 [***E. isola* (Edwards, 1871)**].

Genus ***Cyclargus*** Nabokov, 1945 [***C. ammon* (Lucas, 1857)**, *C. dominicus* (Möschler, 1886), *C. kathleena* Johnson & Matusik, 1992, *C. oualiri* Brévignon, 2002, *C. shuturn* Johnson & Bálint, 1905, *C. sorpresus* Johnson & Matusik, 1992, *C. thomasi* (Clench, 1941)].

Genus ***Pseudochrysops*** Nabokov, 1945 [***P. bornoi* (Comstock & Huntington, 1943)**].

*This taxon seems to include at least two species but distributions and nomenclature are unclear.

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Supporting information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Includes Tables S1–S3 and associated references.

Data S1. Talavera_et_al_2011.nex.

Appendix 1

Description of the new genus Rueckbeilia

Rueckbeilia Lukhtanov, Talavera, Pierce & Vila, gen. nov.

Type species *Lycaena fergana* Staudinger, 1881 (Stett. Ent. Z. p. 262) (type species originally described as "*Lyc.[aena] Loewii* Z. var.? *Fergana* Stgr.").

The name is feminine in gender.

Description

Head with whitish scales. Antennae approximately half as long as fore wing costa, with alternating black and white dots. The antennal club consists of 14 or 15 segments. Dorsal side of the club black with white end, ventral side reddish brown. Second segment of labial palpus white with blackish brush; third segment black. Eyes without hairs, bordered with snow-white scales. Length of fore wing 13–15 mm. Wing colour sexually dimorphic. Male upper side (Fig. 2a) violet-blue; black margin of the wings narrow (0.5–1 mm); veins slightly darkened distally; black discal spot of the fore wing small or unclear. Inner part of cilia dark grey, outer part white. Male underside (Fig. 2b) greyish brown with black spots encircled by white; hindwing with two to four orange submarginal spots; three to fourblack marginal spots near tornus with blue metallic scales. Female upper side brown with two to three orange submarginal spots on hindwing and with cilia as in the male. Female underside almost the same as in the male, but slightly darker.

Male genitalia

Uncus divided into two sclerotized lobes. Gnatos situated at their bases, in the form of sclerotized hooks. Juxta with two long narrow branches. Aedeagus straight and relatively short. Valvae (Fig. 3a) narrow, with a strongly convex and setose longitudinal membranous fold on the ventral wall. The costal margin of the valvae is bent medially, so that a membranous subcostal groove is formed between this margin and the longitudinal fold. Sacculus extends along the entire ventral margin of the valvae. The musculature of male genitalia has been investigated by Stekolnikov (2011), who has found that (i) the transversal intravalval musculature consists of a single undifferentiated muscle, (ii) the fixed insertion site of the intravalval muscle expands over the entire surface of the sacculus, and (iii) the fibres diverge in a radial pattern and attach to both the articular and the costal margin of the valvae.

Female genitalia

Ovipositor rather short. Anterior apophyses three times shorter than posterior ones. Antevaginal plate large, with two sclerotized lobes, and forming a deep concavity with membranous proboscis. Proboscis with a small, strongly sclerotized plate on the top and connected with ductus bursae. Bursa membranous, without signum.

Diagnosis

The external morphology of *Rueckbeilia* is most similar to the genera *Kretania* (especially *K. alcedo*) and *Agriades* (especially *A. optilete*). All these taxa share a similar wing pattern that seems to have evolved independently several times, and a possibly plesiomorphic structure of the male valvae with a well developed membranous median fold. However, *Rueckbeilia* represents a distinct monophyletic entity on the basis of molecular characters. It is not closely related to *Kretania* or *Agriades*, and can be distinguished from these and from other genera by using molecular markers from *COI*, *COII*, *EF-1α*, *Wg*, *ITS2*, *CAD*, *28S*, and *H3* (Table S3, Appendix S1). The mitochondrial diagnostic characters are in the following positions in *COI* + *COII* mtDNA: guanine (G) in position 1801 and thymine (T) in position 2139. For the nuclear marker *Wg*, diagnostic characters are in the following positions: adenine (A) in 217 and G in 222. For the nuclear marker *EF-1α*, diagnostic characters are A in position 295 and T in position 304. For the nuclear marker *CAD*, G in position 413 is a diagnostic character. For the nuclear marker *28S*, diagnostic characters are in the following positions: G in 284 and T in 586. For the nuclear marker *ITS2*, diagnostic characters are in the following positions: cytosine (C) in 12 and 1026 (positions refer to the alignment provided as Supplementary Table S3). Except for these fixed molecular differences that distinguish the genus *Rueckbeilia* from all other genera of the subtribe Polyommatina, there are numerous positions that differentiate the genus *Rueckbeilia* from particular genera (Table S2, Appendix S1). Although these characters are not genus-specific, they constitute unique combinations that can be used for diagnostics.

Distribution

Uzbekistan, Tajikistan, Kyrgyzstan, Kazakhstan, and Northwest China. Records for East Iran and Turkmenistan require verification.

Etymology

The name is given in honour of Eugen Rückbeil and his two sons, Georg and Wasily (second half of the 19th century–beginning of the 20th century, exact years unknown), famous Russian collectors of German origin who explored the butterfly fauna of Central Asia and West China.

Note. In addition to *R. fergana*, we provisionally include in the genus *Rueckbeilia* the phenotypically similar (but genetically still unstudied) taxon *Rueckbeilia rosei* (Eckweiler, 1989) **comb. nov.**, a species known from East Turkey and Iran and traditionally considered within the genus *Vacciniina*.