

Red & black or black & white? Phylogeny of the *Araschnia* butterflies (Lepidoptera: Nymphalidae) and evolution of seasonal polyphenism

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Abstract

Phylogeny of the butterfly genera *Araschnia*, *Mynes*, *Symbrenthia* and *Brensynthia* (Lepidoptera: Nymphalidae: Nymphalini) is reconstructed, based on 140 morphological and ecological characters. The resulting tree shows that *Araschnia* is a sister group of the clade including *Symbrenthia*, *Mynes* and *Brensynthia* (*Symbrenthia* is paraphyletic in the respect of remaining genera; *Symbrenthia hippalus* is a derived species of *Mynes*). The species-level relationships within *Araschnia* are robustly supported as follows: (*A. davidis* (*prorsoides* (*zhangii doris*) (*dohertyi* (*levana burejana*))))). Analysis of the wing colour-pattern characters linked with the seasonal polyphenism in the *Araschnia* species suggests that the black and white coloration of the long-day (summer) generation is apomorphic. Biogeographically, the origin of polyphenism in *Araschnia* predates the dispersal of some *Araschnia* species towards the Palearctic temperate zone, and the ecological cause of the polyphenism itself is then probably not linked with thermoregulation. The possible mimetic/cryptic scenarios for the origin of *Araschnia* polyphenism are discussed.

Introduction

In seasonally polyphenic butterflies, identical genomes produce different phenotypes in response to seasonally predictable environmental cues (Shapiro, 1976, 1984). The phenomenon has for long fascinated biologists, and since the conditions that trigger formation of seasonal forms evinced as experimentally tractable, many physiologically oriented studies investigated the proximate causes of polyphenic developments (e.g. Koch, 1992; Brakefield, 1996; and references therein). In parallel, evolutionists and ecologists were attracted to possible adaptive significance of seasonal morphs (Roskam & Brakefield, 1999; Kemp & Jones, 2001; Hazel, 2002). The fact that diverse phenotypic patterns develop from one genome allowed study of the formation of the patterns at various levels of organization, from genetic to population and inter-specific (Brakefield & French, 1999; Beldade & Brakefield, 2002; McMillan *et al.*, 2002).

The classical example of butterfly seasonal polyphenism is the European Map Butterfly, *Araschnia levana* (Linnaeus, 1758) (Lepidoptera: Nymphalidae). In this species, adults of the May-flying spring generation that develop in short-day environment are reddish with black spots on dorsal surface, whereas long-day adults of the summer generation that fly from July to August are black with a prominent vertical white stripe (Fig. 1). Furthermore, the summer-generation butterflies have larger body size, heavier thorax, lower abdomen to body mass ratio, larger wing area, less pointed wings and lower wing loading, in addition to a more open population structure and greater mobility (Fric & Konvicka, 2000, 2002). The different wing pattern formation in the spring- and summer-generation butterflies is proximately triggered by the timing of ecdysteroid release, which is under photoperiodic control and which is mediated by temperature in the pupal stage (see Koch & Buckmann, 1987; Koch, 1996; Windig & Lammar, 1999). Despite the good knowledge of the proximate mechanisms, the ultimate factors responsible for the polyphenism in *A. levana* remain enigmatic, and further insights into possible adaptive value of the polyphenic development have been hindered by insufficient knowledge of its evolutionary origin.

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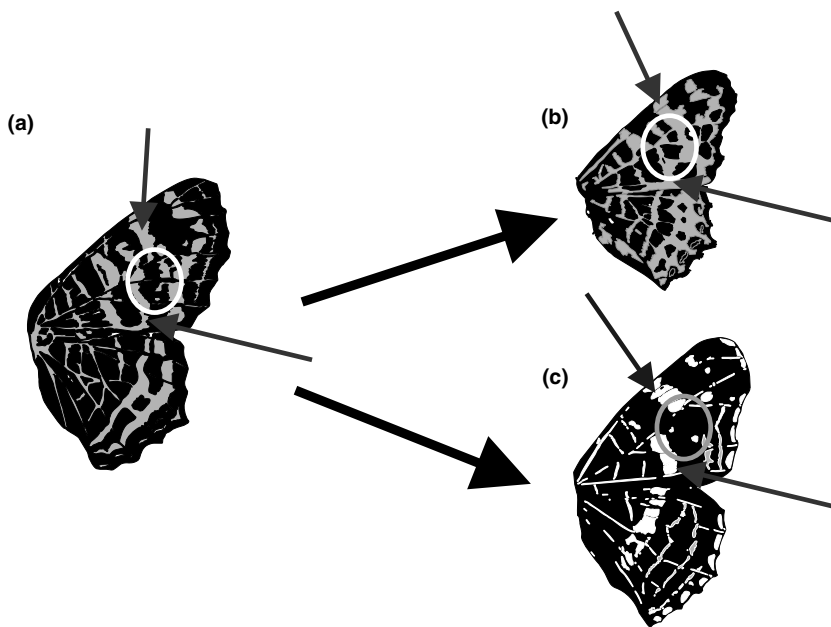


Fig. 1 The proposed evolution of seasonally polyphenic wing patterns in *Araschnia*. (a) Ancestral state (*A. davidis*); (b) *A. levana*, spring generation; (c) *A. levana*, summer generation. The circles indicate the change in extent of dark spots in post-discal area of wings (characters #59 + 60 in Appendix 1, see *Supplementary material*), which is secondarily reduced in the spring generation adults. The arrows indicate the two pattern elements (characters ##73 + 74 and 84 + 85 in Appendix 1, see *Supplementary material*) which attained white colour 'black-and-white' as the derived state in adults of the summer generation.

In this study, we formulate a cladistic hypothesis on evolution of the genus *Araschnia* Hübner, 1819, and its closest relatives, using 140 morphological and ecological traits. Using the tree topology, we ask which of the two seasonal patterns of *Araschnia levana* is the plesiomorphic (primitive) one and which of them is apomorphic (derived) and thus worthy to be explored for possible adaptive value. We supplement the phylogeny with biogeographic analysis, asking which environmental pressures could have influenced origin of the *Araschnia*-type polyphenism.

Materials and methods

Taxon sampling

Understanding the origins of the polyphenism within *Araschnia* has long been hindered by insufficient knowledge of higher-level phylogenetic relationships within the Nymphalidae (see Harvey, 1991; de Jong *et al.*, 1996; Ackery *et al.*, 1999). Recently, there was much progress because of molecular (Janz *et al.*, 1999; Brower, 2000; Wahlberg *et al.*, 2003) and total evidence (Nylin *et al.*, 2001) phylogenies of the Nymphalini, a nymphalid subgroup including *Araschnia*. The new findings showed that *Araschnia* groups with *Mynes* Boisduval, 1832 and *Symbrenthia* Hübner, 1819, forming a monophyletic clade herein referred to as '*Araschnia*-clade'. However, since the previous studies primarily focused on the clade sister to the *Araschnia*-clade (Janz *et al.*, 2001) and on higher-level relationships (Wahlberg & Nylin, 2003), they included only one species per genus within the *Araschnia*-clade, and thus could not resolve questions on the evolution of seasonal polyphenism in *Araschnia*.

There is no recent authoritative revision for the taxa of the *Araschnia*-clade, and, as is often the case in butterflies, synonyms and *nomina nuda* abound in literature. Hence, it is difficult even to specify the exact number of valid species. The situation is complicated by distribution of many of the species in hardly accessible Asian regions (e.g. in Tibet) and by the resulting scarcity of material. Recent literature (e.g. Holloway, 1973; D'Abbrera, 1977, 1984, 1992; Io, 1994; Parsons, 1999; Huang, 2000) recognizes at minimum seven species of *Araschnia*, all of them with Palaearctic distribution, 10 species of *Mynes* distributed in Australia, New Guinea and the Moluccas, and 10–15 species of *Symbrenthia* occurring mainly in the Oriental region, two of them considered by Huang (2000) to form a separate genus *Brensynthia* (Table 1). We included most of these species in our analyses, except for the recently described *M. obiana* Rawlins & Tennet, 2003 (described from the Moluccas), the little-known *Symbrenthia silana* de Nicéville, 1885 (Sikkim) and *S. hysudra* Moore, 1874 (Kashmir). Two Oriental taxa, *S. anna* Semper, 1888 and *S. javanus* Staudinger, 1896, regarded by some authors (see Corbet, 1948; Corbet & Pendlebury, 1992; Io, 1994) as taxonomically questionable, were also excluded.

For outgroup comparison, we used 13 species of nymphalid butterflies (Table 1), viz., *Brenthis ino* (Heliconiinae), *Melitaea athalia* (Nymphalinae: Melitaeini) and 11 species of the Nymphalini; we preferred those Nymphalini species studied by Nylin *et al.* (2001).

Characters

We extended the morphological data matrix of Nylin *et al.* (2001) for additional 26 taxa of the *Araschnia*-clade, adding 42 characters and deleting four characters that

Table 1 List of taxa used in the phylogenetic analysis and respective sources of data (NL, Museum Naturalis Leiden; SM, Silesian Museum Opava).

Taxon outgroups	Origin of used data
<i>Brenthis ino</i> (Rottemburg, 1775)	Niculescu (1965), orig.
<i>Melitaea athalia</i> (Rottemburg, 1775)	Niculescu (1965), orig.
<i>Antanartia schaeneia</i> (Trimen, 1879)	Howarth (1966)
<i>Hypanartia lethe</i> (Fabricius, 1793)	Willmott <i>et al.</i> (2001), orig.
<i>Cynthia cardui</i> (Linnaeus, 1758)	Niculescu (1965), Field (1971), Nakanishi (1988), orig.
<i>Inachis io</i> (Linnaeus, 1758)	Niculescu (1965), Nakanishi (1988), orig.
<i>Aglais urticae</i> (Linnaeus, 1758)	Niculescu (1965), Nakanishi (1988), Miller & Miller (1990), orig.
<i>Aglais cashmirensis</i> (Kollar, 1844)	orig.
<i>Aglais milberti</i> (Godart, 1819)	Shull (1987), Miller & Miller (1990)
<i>Nymphalis polychloros</i> (Linnaeus, 1758)	Miller & Miller (1990), orig.
<i>Roddia vaualbum</i> (Dennis & Schiffmüller, 1775)	Kawazoe & Wakabayashi (1981), Nakanishi (1988), Miller & Miller (1990)
<i>Kaniska canace</i> (Linnaeus, 1763)	Shirozu (1960), Nakanishi (1988)
<i>Polygonia c-album</i> (Linnaeus, 1758)	Niculescu (1965), Nakanishi (1988), orig.
<i>Araschnia</i> Hübner, 1819	Stichel (1906a), Fruhstorfer (1927a), D'Abbrera (1992)
<i>A. levana</i> (Linnaeus, 1758)	Niculescu (1965), Kawazoe & Wakabayashi (1981), Fukuda <i>et al.</i> (1985), Nakanishi (1988), orig. Paulus
<i>A. burejana</i> (Bremer, 1861)	Kawazoe & Wakabayashi (1981), Fukuda <i>et al.</i> (1985), Io (1994), orig. SM
<i>A. proroides</i> (Blanchard, 1871)	Io (1994), orig. NL, Paulus
<i>A. davidis</i> Poujade, 1885	Io (1994), orig. NL
<i>A. doris</i> Leech, 1893	Io (1994), orig. NL
<i>A. dohertyi</i> Moore, 1899	Io (1994)
<i>A. zhangi</i> Chou, 1994	Io (1994)
<i>Brensynthia</i> Huang, 2000	Holloway (1973), D'Abbrera (1984), Io (1994), Huang (1998, 2000)
<i>B. niphanda</i> (Moore, 1872)*	orig. NL
<i>B. sinoides</i> (Hall, 1935)*	orig. NL
<i>Symbrenthia</i> Hübner, 1819	de Nicéville (1902), Stichel (1906b), Fruhstorfer (1927b), Holloway (1973), D'Abbrera (1984), Mani (1986), Nakanishi (1988), Io (1994)
<i>S. lilaea</i> (Hewitson, 1864)	Corbet & Pendlebury (1992), orig. SM
<i>S. brabira</i> Moore, 1872	Huang (1998), orig. NL
<i>S. leoparda</i> Chou & Li, 1994	Huang (1998)
<i>S. hypatia</i> (Wallace, 1869)	Schroeder & Treadaway (1979, 1998), Corbet & Pendlebury (1992), orig. NL
<i>S. dalailama</i> Huang, 1998	Huang (1998)
<i>S. hypselis</i> (Godart, 1823)	Sevastopulo (1947), Shirozu (1960), Corbet & Pendlebury (1992), Igarashi & Fukuda (1997), Huang (1998), orig. SM
<i>S. hippalus</i> (Felder, 1867)	orig. NL
<i>S. hippoclus hippoclus</i> (Cramer, 1779)	Shirozu (1960), Corbet & Pendlebury (1992), Igarashi & Fukuda (1997), orig. SM
<i>S. hippoclus hylaeus</i> (Wallace, 1869)†	orig. NL
<i>S. viridilunulata</i> Huang, 1999	Huang (1999)
<i>S. plateni</i> Staudinger, 1896	orig. NL
<i>S. intricata</i> Fruhstorfer, 1897	
<i>Mynes</i> Boisduval, 1832	Fruhstorfer (1927c), Vane-Wright (1976), D'Abbrera (1977), Tsukuda (1985), Parsons (1999)
<i>M. plateni</i> Staudinger, 1877*	orig. NL
<i>M. doubledayi</i> Wallace, 1869*	orig. NL
<i>M. talboti</i> Juriaanse & Volbreda, 1922*	
<i>M. eucosmetos</i> Godman & Salvin, 1879*	
<i>M. geoffroyi</i> (Guérin-Méneville, 1831)*	Fruhstorfer (1909), Braby (2000), Igarashi & Fukuda (2000), orig. SM
<i>M. katharina</i> Ribbe, 1898*	
<i>M. websteri</i> Grose-Smith, 1894*	orig. SM
<i>M. anemone</i> Vane-Wright, 1976*	Vane-Wright (1976)
<i>M. aroensis</i> Ribbe, 1900*	
<i>M. woodfordi</i> Godman & Salvin, 1888*	Ribbe (1897), orig. NL

*The phylogenetically consistent nomenclature (see *Discussion*) for the marked species of '*Brensynthia*' is as follows: *Symbrenthia niphanda* Moore, 1872; and *Symbrenthia sinoides* Hall, 1935; for the species of '*Mynes*', it is: *Symbrenthia plateni* (Staudinger, 1877) comb. nov.; *Symbrenthia doubledayi* (Wallace, 1869) comb. nov.; *Symbrenthia talboti* (Juriaanse & Volberda, 1922) comb. nov.; *Symbrenthia eucosmetos* (Godman & Salvin, 1879) comb. nov.; *Symbrenthia geoffroyi* (Guérin-Méneville, 1831) com. nov.; *Symbrenthia katharina* (Ribbe, 1898) comb. nov.; *Symbrenthia websteri* (Grose-Smith, 1894) comb. nov.; *Symbrenthia anemone* (Vane-Wright, 1976) comb. nov.; *Symbrenthia aroensis* (Ribbe, 1900) comb. nov.; *Symbrenthia woodfordi* (Godman & Salvin, 1888) comb. nov.

† The taxon should be raised to the full-species status, as it is not a sister species of *S. hippoclus hippoclus*, but of the broad clade *S. plateni* + *S. hypselis*-group + '*Mynes*' group (supported by a large process from an outer margin of the hindwing near Cu1, distinct expansion of the hindwing margin posterior to M3, loss of the contrasting coloration of the ventral forewing veins, and ventral hindwing medial system D and ventral forewing symmetry system G both interrupted by the veins). Originally described as *Laozona hylaeus* Wallace, 1869, its proper name is *Symbrenthia hylaeus* (Wallace, 1869).

were uninformative for the species sample currently analysed. The morphological data were obtained either by studying collection specimen, or from literature (see Table 1). The bulk of museum specimens came from the Silesian Museum, Opava, Czech Republic, and Naturalis, Leiden, the Netherlands. The data matrix contained 133 cladistically informative morphological and seven ecological traits for 45 species (characters: Appendix 1; data matrix: Appendix 2; see *Supplementary material* or <http://www.zoo.bf.jcu.cz/data/araschnia>).

We coded the wing-pattern characters using the homology system called 'nymphalid ground plan' or NGP (Nijhout & Wray, 1986; Nijhout, 1991, and references therein), a diagrammatic system that allows the identification of homologous pattern elements across different taxa of Lepidoptera. NGP is based on the discovery that the diversity of pigmentation of lepidopteran wings can be reduced to a relatively few elements that are repeated in each wing cell (see McMillan *et al.*, 2002). The homology and terminology of genital traits follow Niculescu (1965).

Coding of polyphenic traits

In seasonally polyphenic species of *Araschnia*, three characters attain different states in different generations (Fig. 1). (1) The colour of the anterior spot or band immediately distad of central symmetry system on the dorsal forewing is reddish in spring and white in summer (character #73). (2) The background colour outside the central symmetry system in the posterior part of the dorsal side of the forewing is again reddish in spring and white in summer (#84). We herein refer to the wing patterns created by combination of these characters as to 'reddish' and 'black-and-white', respectively. Finally, (3) the relative extent of black spots on postdiscal (outer) parts of the wings (#59) is reduced in the spring generation, resulting in the 'light' appearance, as opposed to the 'dark' appearance of the summer generation. The three traits repeat themselves on the hindwings, and account for the dramatic differences between seasonal morphs (see Nijhout, 1991; Windig & Lammar, 1999).

As various treatments of the polyphenic traits could influence the topology of resulting trees, we used three alternative coding approaches.

1. In the *basic coding*, each of the above three characters was duplicated, which gave one character for the first and one for the second generation in all species that have more than one generation per year (characters #59 + 73 + 84, and 60 + 74 + 85, respectively, in Appendix 1, see *Supplementary material*). In the monomorphic multivoltine (= more-generation) butterflies, these characters achieved in fact the weight of two. However, we could not resolve *a priori* which of the seasonal patterns was homologous with the patterns in univoltine (= one-generation) species. To overcome

this uncertainty, we created two alternative data matrices, in which we coded the patterns of the univoltine species either as the 'first' generation, or as the 'second' one, and filled the empty columns for the 'non-existent generation' by question marks.

2. In *polymorphic coding*, all the characters attaining different states in different generations were simply coded as 'polymorphic'.
3. '*Separate species coding*' considered the seasonal forms of the polyphenic species as separate terminals 'species' that shared all monomorphic traits but differed in the polyphenic wing pattern characters.

Tree building and character optimization

The data matrices were analysed using the maximum parsimony program NONA version 2.0 (Goloboff, 1999; option 'hold 100000; mult*100; hold/100', using the unconstrained 'mult*max*' search strategy). Support of individual branches was assessed by calculating Bootstrap support values (1000 replications; NONA), Jackknife Monophyly Index (Random Cladistics; Siddal, 1995) and Bremer support (NONA: option 'bsupport 100000') for the basic-coded dataset. Because butterfly wing pattern traits are obvious candidates for convergent evolution, we then re-ran the analyses, separately for each method of coding of polyphenic characters, with matrices that contained all traits except the wing patterns, and with matrices containing the wing patterns only.

The morphological characters responsible for the occurrence of seasonal polyphenism in *Araschnia* ('reddish' vs. 'black-and-white' and 'light' vs. 'dark') and the polyphenism itself were mapped on the resulting trees, using the parsimony optimization procedure (Maddison, 1989), to reconstruct their ancestral states in the *Araschnia*-clade.

Biogeography

Data on distribution within the Oriental region were taken from Holloway (1973). For distributions outside of the Oriental region, we delimited an additional 10 areas (Appendix 3, see *Supplementary material*) using information from the literature (Table 1).

To reconstruct distribution of ancestors of the recent representatives of the *Araschnia*-clade, we employed dispersal-vicariance analysis (DIVA; Ronquist, 1996), a method in which ancestral distributions are inferred from a three-dimensional cost matrix based on a simple biogeographic model. DIVA allows the dispersal events as well as vicariant ones, and compared with the 'maximum vicariance' approaches (like Brooks Parsimony Analysis; see Humphries & Parenti, 1999, and references therein), it is possible to reconstruct the reliable distribution history of individual groups even in the absence of a general hypothesis on the area relationships.

Results

Phylogeny of the *Araschnia*-clade

The complete data matrix ('basic coding' of the polyphenic characters) provided 11 most parsimonious trees (length 528, consistency index CI = 0.34, retention index RI = 0.70; Fig. 2). *Araschnia* forms a monophyletic group supported by nine wing-pattern synapomorphies (forewing vein R2 separating distally to the discal cell, veins on the ventral side of fore- and hindwings lightly coloured and interrupting colour-pattern symmetry systems D, F, G and I, a median eye spot on dorsal forewing, and posteriorly situated blue spots adjoining the hindwing margin). However, all these synapomorphies are homoplasious and are present also in other nymphalids. *Araschnia davidis* (Tibet; life cycle unknown) is the most basal species of the genus. The clade of six *Araschnia* species aside from *A. davidis* is well supported by three synapomorphies, one of them nonhomoplasious (the space between symmetry systems F and G on the ventral hindwing is wide and white- to yellow-coloured). The relationships between the rest of *Araschnia* species are less strongly corroborated. Three clades seem to exist – basal *A. proroides* (China, Tibet and northern India; life cycle unknown), the *doris-zhangii* clade (China; polyphenism present in *A. doris*, unknown in *A. zhangii*), and the *dohertyi*-(*levana-burejana*) clade (*A. dohertyi* from China and northern India, *A. burejana* from the eastern Palaearctic, *A. levana* from the entire northern Palaearctic; all polyphenic). *Araschnia levana* and *A. burejana* share a single homoplasious synapomorphy (outer ocellar symmetry system I present but interrupted on veins on ventral forewing). Moreover, they are the only species of the *Araschnia*-clade that inhabit northern areas of the Palaearctic Realm. The species' relationships within *Araschnia* were not affected by the different character coding procedures.

The sister branch of *Araschnia* consists of *Mynes*, *Brensymthia* and *Symbrenthia* ('*Symbrenthia*-subclade' hereinafter), corroborated by four wing-pattern synapomorphies. There are two well-supported groups within the subclade above the basal, weakly supported asymmetrical 'ladder' of numerous individual *Symbrenthia* species (such as *S. intricata* and *S. hippoclus*). One of these derived groups, herein called the '*Mynes*-group', contains all *Mynes* species plus *S. hippalus*. The other group includes *Brensymthia* plus the five species of *Symbrenthia* that all share the pattern of symmetry systems being discontinuous near major veins on the ventral wing surfaces (herein '*S. hypselis*-group') (Fig. 3).

Monophyly of the whole *Araschnia*-clade is supported by three wing-pattern, one genitalic and three larval synapomorphies. The positions of the outgroup Nymphalini taxa agreed well with findings of Janz *et al.* (1999) and Nylin *et al.* (2001) who have supported the sister-group relationship between the *Araschnia*- and Nymphalini-

clades on the basis of morphological characters. However, the recent combined analysis by Wahlberg & Nylin (2003), based on four genes and morphology, suggests that the *Araschnia*-clade is more deeply nested within the Nymphalini, with *Antanartia* being a sister group of the *Araschnia*-clade.

The two alternatives of 'basic coding' of the polyphenic characters in univoltine butterflies (i.e. as either the 'first', or the 'second' generation) did not influence tree topology. If the 'polymorphic' coding was applied, the topology was identical to that derived from the 'basic coding'. The 'separate species' coding resulted in the basal polytomy: *Araschnia* + *S. intricata* + the rest of the *Symbrenthia*-subclade.

Exclusion of wing-pattern characters from the basic data matrix resulted in 501 equally parsimonious trees (length 241, CI 0.38, RI 0.68; Fig. 4a). The strict consensus includes the monophyletic *Araschnia*-clade, which is split into *Symbrenthia intricata* + *Araschnia*-subclade, and to the rest of the *Symbrenthia*-subclade. Within *Araschnia*, only the *doris-zhangii* clade is retrieved.

The analysis restricted exclusively to the wing pattern attained rather good resolution, yielding 18 most parsimonious trees (length 262, CI 0.34, RI 0.74; Fig. 4b). This subset of data does not support monophyly of the whole *Araschnia*-clade, as the *Mynes*-group joins with *Araschnia* and with nymphaline outgroup genera *Antanartia* and *Cynthia*. However, the *Araschnia* species relationships are well resolved and not in conflict with the relationships derived from the complete dataset. *Araschnia* thus retains its position as a sister group of the *Symbrenthia* and *Mynes* butterflies even after exclusion of wing pattern characters, but loses the position in the analysis based on wing patterns only. Clearly, the wing-pattern traits are responsible for the changed topology, which allows inferring that the sister-group relationship between the *Araschnia*- and *Symbrenthia*-subclades is not due to convergence in wing-pattern traits. Also, the different positions of *Mynes* in the two analyses supports the notion that this group evolved as a derived branch within the *Symbrenthia*-subclade, whose members lost the *Symbrenthia*-like transversally striped wing pattern (Fig. 3c, d).

Seasonal polyphenism

The parsimony optimization of character states on the strict consensus of trees indicates (irrespective of the method of polyphenism coding) that the seasonal polyphenism originated repeatedly within the Nymphalini: once as an autapomorphy of *Polygonia*, and twice or three times within the *Araschnia*-clade (Fig. 5). In the latter clade, the seasonal polyphenism either originated in an ancestor of the entire *Araschnia*-clade, then disappeared in the *Symbrenthia*-subclade just above the branching off *S. lilaea*, and finally re-appeared in the ancestor of the *S. hypselis*-group; or, alternatively, the polyphenism

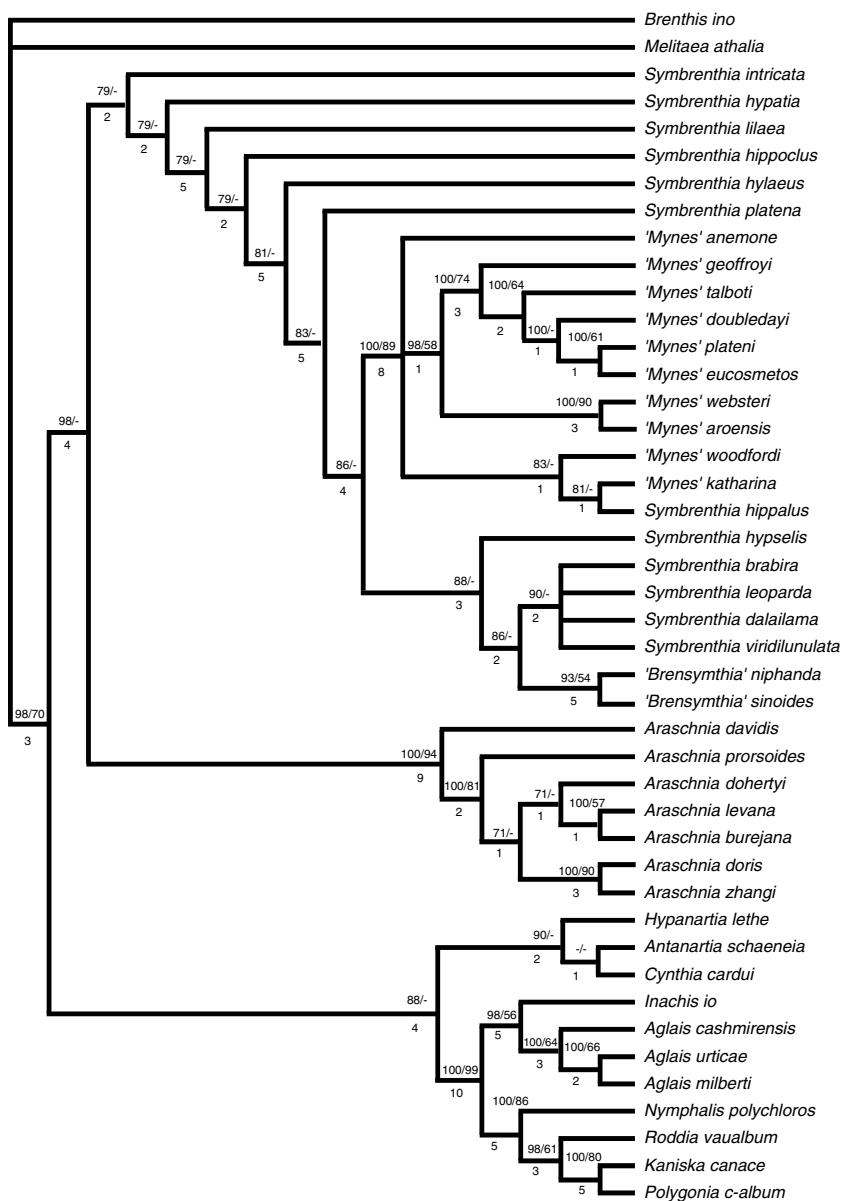


Fig. 2 Cladistic relationships of the *Araschnia*-clade. Jackknife monophyly indices/bootstrap values are shown above the nodes, Bremer indices are shown below the nodes.

evolved three times independently: in *S. lilaea*, in the *S. hypselis*-group, and in *Araschnia*.

The former scenario assumes that the seasonal polyphenism in all branches of the *Araschnia*-clade represents a homologous feature. However, the three instances of polyphenism within the *Araschnia*-clade are associated with different modes of wing-pattern restructuring. In *Araschnia*, it is associated with two autapomorphic character states that seem to have appeared in the ancestor of the genus: (a) the appearance of the white ground colour on dorsal wings in the long-day adults (character #73:0), and (b) the reduction of the black pigmentation on post-discal fields, resulting in 'light' patterns of the short-day adults (#59:0). Whereas the red

ground colour is present in ancestors of the *Araschnia*-clade, the white coloration is a true evolutionary novelty. On the contrary, in the polyphenic *Symbrenthia* species the polyphenism is not accompanied with such a radical restructuring of the wing pattern, but rather with varying the relative extends of reddish and dark coloration.

Biogeography

The DIVA analysis (Fig. 6) shows that ancestor of the *Araschnia*-clade was widely distributed in the southern Palaearctic, Oriental and New Guinean regions. However, it was absent in northern areas of the Palaearctic region (i.e. Manchuria, Siberia, Japan and Europe), and

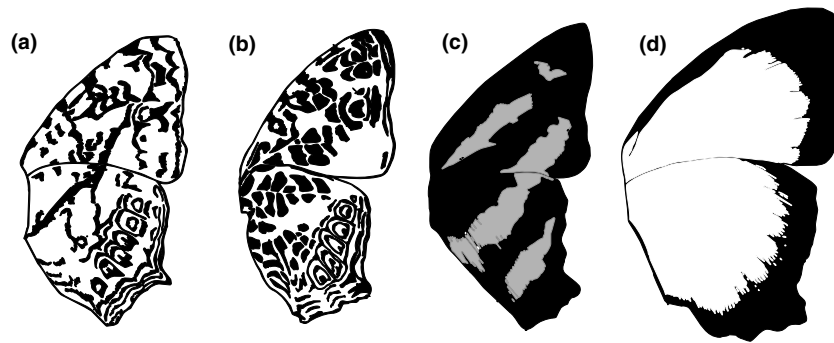


Fig. 3 Distinct types of general wing patterns found in the *Symbrenthia*-subclade. (a) *Symbrenthia hippoclus*, ventral wing surface. Ancestral state with majority of the symmetry-system elements continuous on wing veins. (b) *Symbrenthia hypselis*, ventral wing surface. Derived state, typical for the *S. hypselis*-group, with the symmetry system elements interrupted by wing veins. (c) *Symbrenthia hypselis*, dorsal wing surface. Striped reddish-and-dark pattern found in basal species of the genus plus in the *S. hypselis*-group. (d) *Mynes geoffroyi*, dorsal wing pattern. Large unicoloured fields resembling *Delias* pierids.

on the Australian continent. The ancestor of *Araschnia* occurred in China, whereas the ancestor of the *Symbrenthia*-subclade was distributed as widely as the *Araschnia*-clade ancestor. The northern-Palaeartic distribution of *A. levana* and *A. burejana* was caused by the northward dispersal from China. In the *Symbrenthia*-subclade, the *S. hypselis*-group radiated in the mainland Oriental region, the Greater Sundas, and southern China. The ancestor of the *Mynes*-group originated in the Papuan subregion and subsequently dispersed to Australia (*M. geoffroyi*), the Moluccas (e.g. *M. talboti*), and Sulawesi (*S. hippalus*).

Discussion

Phylogenetic systematics of the *Araschnia*-clade

Our results document sister-group relationship between monophyletic *Araschnia* and the *Symbrenthia*-subclade containing species traditionally included to *Symbrenthia* and *Mynes*. The *Mynes* species (plus *S. hippalus*) form a derived group within the *Symbrenthia*-subclade, with sister-group relationship to the *S. hypselis*-group. It follows that conserving the generic name *Mynes* renders *Symbrenthia* paraphyletic (even if *S. hippalus* is not considered) and all the constituent species should be included under the older generic name *Symbrenthia*. The same applies to the generic name *Brensymthia* Huang, 2000, as the butterflies in question form a derived branch within the *S. hypselis*-group. The phylogenetically consistent nomenclature of the *Araschnia*-clade butterflies is included in Table 1.

Biogeography of *Araschnia*

The ancestral area reconstruction indicated that the two main lineages of the *Araschnia*-clade radiated in different directions. Whereas the *Symbrenthia*-subclade radiated,

through a succession of vicariance events, in Oriental and Australian regions, the ancestor of *Araschnia* inhabited a boundary zone between the mainland-Oriental and Palaeartic regions.

The northern Palaeartic temperate distribution of the *A. levana*-*A. burejana* clade is clearly derived and dispersal-based. The role of dispersal in the evolution of *Araschnia* is supported by ecology of recent species as well. One of the northern species, *A. levana*, is a good disperser with an open population structure (Eric & Konvicka, 2000) and has colonized considerable parts of Europe during the past century (Hrubý, 1956; van Swaay, 1990).

As the origin of polyphenism in the ancestral *Araschnia* predated the dispersal of a few species towards the northern temperate regions, an ecological cause of the phenomenon should not be sought in 'temperate' alternation of cold and of warm seasons, but in conditions likely to have existed in the ancestral areas. In this respect, it is notable that basalmost species of *Araschnia* (*A. davidis* and *A. prorsoides*) occur in mountainous regions at the boundary between Palaeartic and Oriental realms (i.e. Tibet, Yunnan and northeastern India) (e.g. D'Abbrera, 1992; Io, 1994). Although little is known about their specific habitats (do they occur in high altitudes, or in subtropical valleys of these topographically and climatically diverse regions?), it is clear that these regions are seasonal with respect both to the climate (alternation of dry and wet monsoon seasons) and photoperiod. Moreover, the same regions harbour derived representatives of the *S. hypselis*-group, which are all polyphenic, in contrast to basal monomorphic species of the *Symbrenthia*-subclade that inhabit the aseasonal tropics (e.g. Hagen, 1896; Parsons, 1999). These sub-tropical species of *Symbrenthia*, despite living outside of the tropics, exhibit a 'tropical' pattern of polyphenism (cf. Brakefield & Larsen, 1984; Nijhout, 1991): they are darker (or at least duller) in the dry season and brighter in the wet season (Mani, 1986).

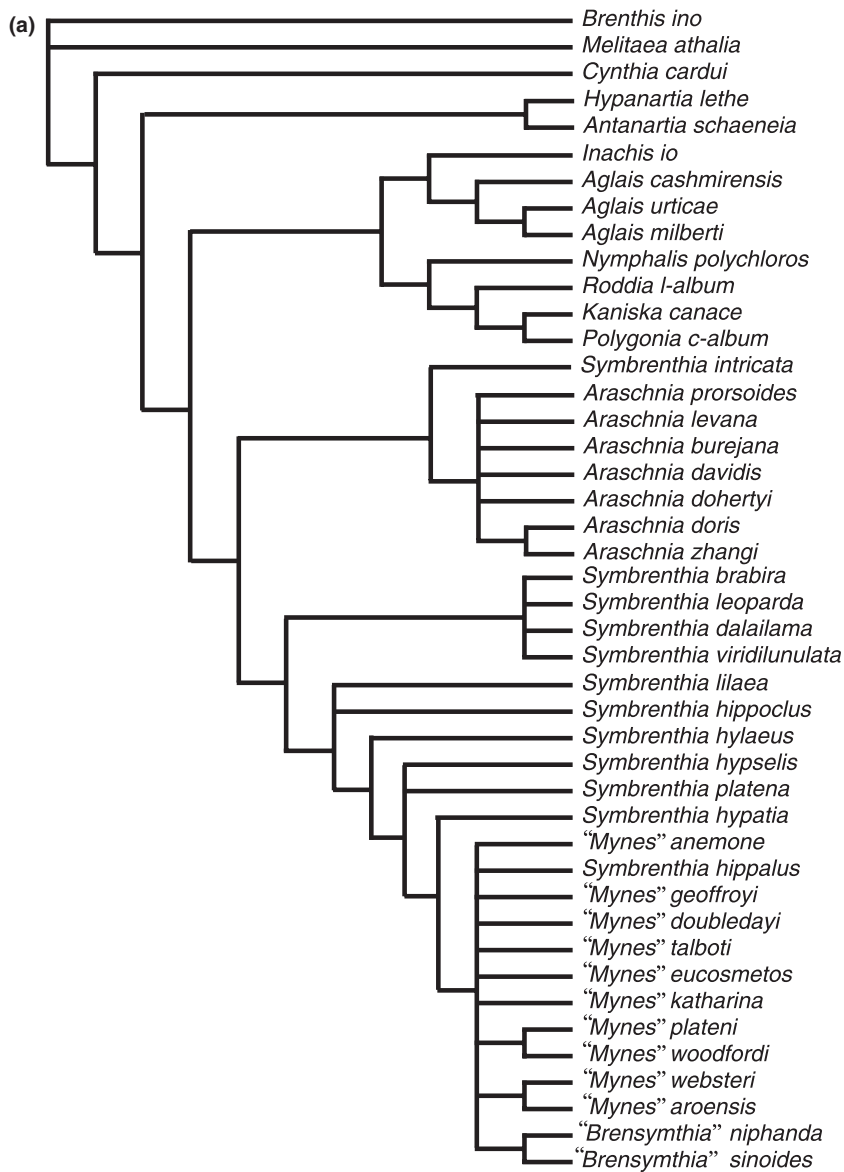


Fig. 4 Phylogeny of the *Araschnia*-clade constructed from partial data matrices. (a) Wing-pattern characters excluded. (b) Only wing-pattern characters included.

Assuming, tentatively, subtropical distribution of common ancestors of present-day *Araschnia*, and considering the pattern of polyphenism found in co-existing species of the *S. hypselis*-group, we suggest the following speculative scenario of origin of *Araschnia* polyphenism. The ancestor of *Araschnia* had become polyphenic in response to a predictable environmental variation experienced in its area of distribution. Judging from present conditions in the subtropics, the likely candidate for the variation would be humidity. The polymorphism became associated with a photoperiodic cue, which could have allowed the northward-dispersing descendants to use this cue for alternating between generations living in cooler (spring) and warmer (summer) conditions. If such a scenario was valid, the striking polyphen-

ism in wing pattern would represent a 'ghost of selection past', whose origin predated colonization of northern parts of the Palearctic Realm.

Polyphenism and evolution of wing patterns

The origin of polyphenism in ancestral *Araschnia* was accompanied by two evolutionary novelties in wing pattern – reduction of dark pigmentation leading to the light reddish spring phenotypes, and origin of the white spots/stripes leading to the black-and-white summer phenotypes. Whereas the light pattern did not deviate much from the ancestral wing coloration in the whole *Araschnia*-clade, the black-and-white pattern of the summer generation required radical repatterning of the

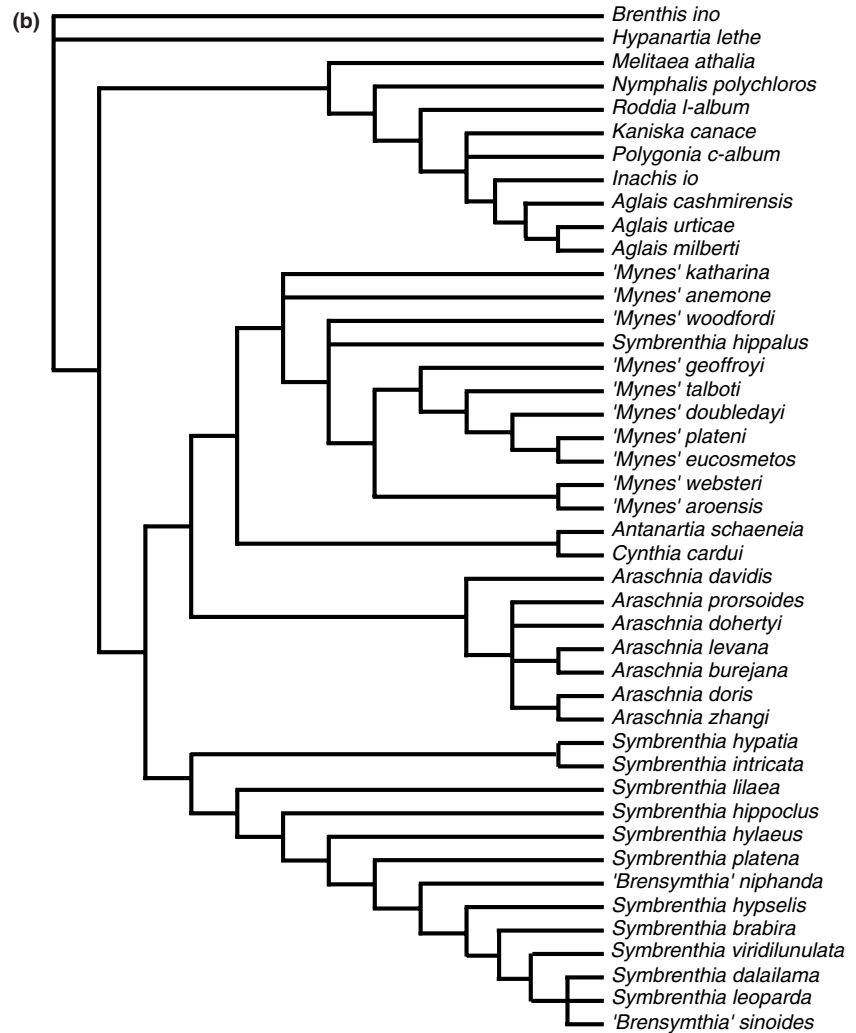


Fig. 4 Continued.

wing coloration, and thus is the prime candidate for an adaptive explanation.

Two interpretations of evolution of wing patterns most commonly encountered in the lepidopterist literature concern thermoregulation and predator avoidance. Regarding thermoregulation, the intriguing point is that temperate species of *Araschnia* are *darker* in summer. This seems counterproductive, because darker wings provide more rapid heating (Heinrich, 1986). However, we have already argued that the dark pattern had likely originated prior to the northward dispersal, in subtropical regions with alternating dry and wet seasons.

Phenomena related to predator avoidance, such as warning/mimetic coloration or crypsis, are increasingly accepted as the driving force behind evolution of wing patterns in Nymphalidae (e.g. Bowers, 1981; Owen *et al.*, 1994; Mallet & Gilbert, 1995; Roskam & Brakefield, 1996; Jiggins *et al.*, 2001). Within the *Araschnia*-clade, larval gregaric habits, host plants, and the conspicuously reddish

wing coloration (ancestral to the clade and still found in basal *Symbrenthia* and short-day *Araschnia*) all suggest their limited palatability (see Rydell *et al.*, 2001; Hagen *et al.*, 2003). Moreover, conspicuous mimetic phenomena occur in '*Mynes*' species, which mimic unpalatable *Tellervo* danaiids and *Delias* pierids (cf. Vane-Wright, 1976; Orr, 1999). However, warning or mimetic phenomena can hardly explain the derived black-and-white pattern in the summer generation. It is often assumed that such patterns provide disruptive concealment, but the assumption has rarely been tested (Silberglied *et al.*, 1980; Brakefield *et al.*, 1992). Several butterfly examples allow to infer that the cryptic disruptive patterns are favoured over warning coloration in relatively arid conditions. A striking example are polyphenic nymphalids of the genus *Precis* Hübner, 1819, especially African *Precis octavia* (Cramer, 1877), which is conspicuously red in the wet season and (disruptively?) black-and-blue in the dry season (cf. Nijhout, 1991). Although we rely on a sheer speculation,



Fig. 5 Parsimony optimisation of the seasonal polyphenism on the *Araschnia*-clade tree. Only the species in which polyphenism is reliably known as present/absent are included, but topology of the all-species tree (Fig. 2) has been preserved. The polyphenic species are shaded. The circles stand for the origins (shaded) and losses (open) of the polyphenism (if it is regarded as ancestral for the whole *Araschnia*-clade). The dark shaded sectors of the tree show origins of the polyphenism according to the more plausible scenario of three independent origins of polyphenism in the clade.

the black-and-white pattern of summer-form *Araschnia* becomes less enigmatic if we assume its origin in seasonally arid conditions. It is also intriguing that black-and-white patterns superficially resembling the summer-form *Araschnia* prevail in the Palaearctic (as opposed to the Oriental) representatives of the nymphalid tribe Neptini (see Kurentsov, 1970). Perhaps, a common environmental pressure influenced the evolution of the black-and-white patterns in both lineages in northern regions of Eurasia.

Our speculation that aposematic/mimetic coloration in ancestral taxa of the *Araschnia*-clade has changed into disruptive/cryptic coloration in the summer forms of *Araschnia* in areas with seasonally varying humidity is

hindered by critically poor knowledge of many aspects of the scenario. It is not conclusively known whether Oriental species of *Symbrenthia* are indeed aposematic functionally. There is lack of information concerning the number of generations and presence of the polyphenism in many species of the *Araschnia*-clade, and the present cladistic hypothesis about the origins of polyphenism within this clade might be incorrect in some details. Finally, there is urgent need to test experimentally whether the black-and-white pattern of summer-generation *Araschnia* indeed renders an advantage of disruptive concealment to the butterfly.

Nonetheless, the findings that origin of the seasonal polyphenism in *Araschnia* predated dispersal of the

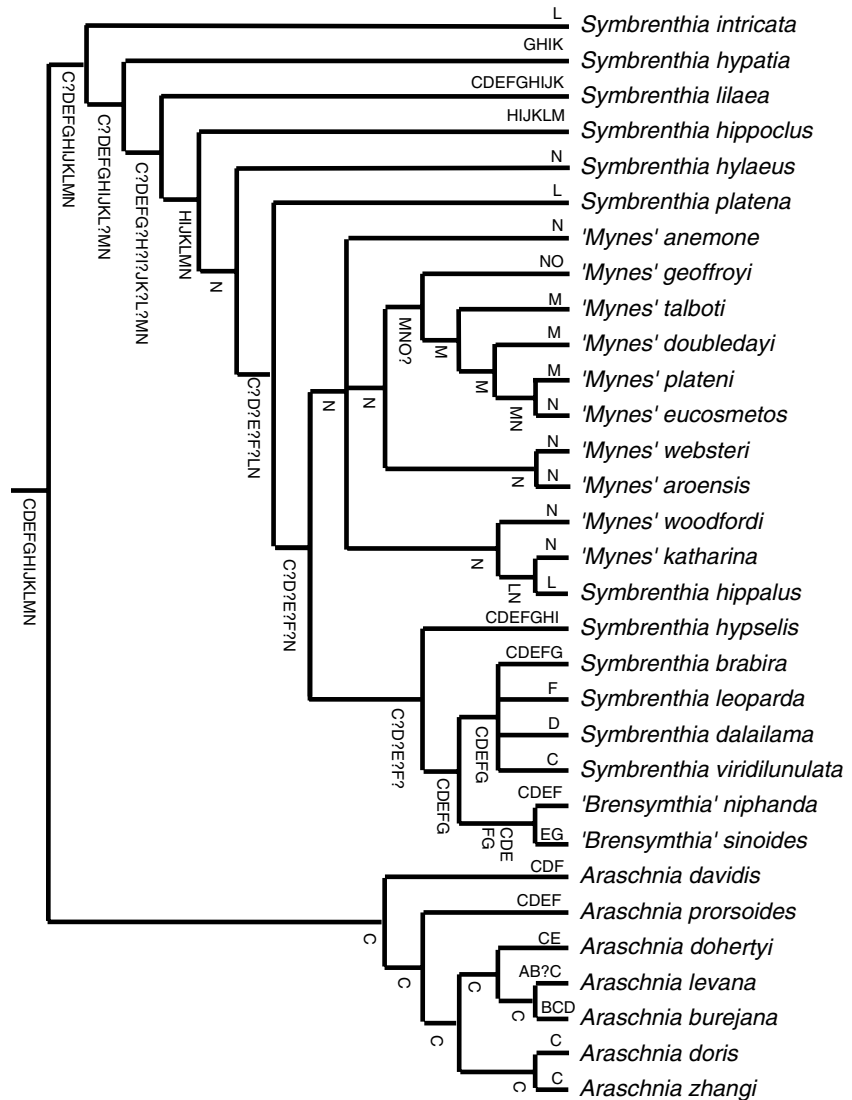


Fig. 6 Reconstruction of distribution of ancestors of the recent representatives of the *Araschnia*-clade by dispersal-vicariance analysis. The capital letters below tree nodes denote areas of ancestral distributions preferred by dispersal-vicariance, the capital letters above terminal branches denote recent distribution. Uncertainties are denoted by question marks immediately following letters for the uncertain areas (e.g. 'CDE?' = ancestor present in areas C, D and possibly E). The areas are as follows: A, Euro/Siberia; B, Manchuria + Japan; C, China; D, Tibet; E, India; F, Yunnan; G, Indochina; H, Malaya; I, Greater Sundas; J, Lesser Sundas; K, Philippines; L, Sulawesi; M, Moluccas; N, New Guinea; O, Australia. See Appendix 2 (*Supplementary material*) for details.

butterflies towards the northern areas, and that the black-and-white pattern is derived in the clade, are well supported. The black-and-white coloration of long-day butterflies deserves further exploration for its possible adaptive value. It is notable that similar black-and-white patterns are relatively frequent in the Nymphalidae and often occur in lineages that contain aposematic species as well. A survey of the relative distributions of these two contrasting patterns in relation to phylogeny of the individual nymphalid clades and their geographical origin is urgently needed.

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Supplementary material

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/jeb/jeb681/jeb681sm.htm>

Appendix A1 List of morphological and ecological characters used for reconstruction of phylogeny of the *Araschnia*-clade. Unless otherwise stated, the multistate characters are unordered ('non-additive').

Appendix A2 Matrix of character states of *Araschnia*-clade butterflies and outgroups.

Appendix A3 Data matrix for DIVA analysis of biogeography of the *Araschnia* clade.

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