

Cladistic analysis of the Neotropical butterfly genus *Adelpha* (Lepidoptera: Nymphalidae), with comments on the subtribal classification of Limenitidini

KEITH R. WILLMOTT

Department of Entomology, The Natural History Museum, London, U.K.

Abstract. A two-stage cladistic analysis of 114 characters from adult and immature stage morphology provided phylogenetic hypotheses for the diverse Neotropical nymphalid butterfly genus *Adelpha* Hübner. Higher-level cladistic relationships were inferred for thirty *Adelpha* species and twenty other species of Limenitidini, confirming the monophyly of *Adelpha* as currently conceived and indicating several montane Asian species as potential sister taxa for the genus. Cladistic relationships between all eighty-five *Adelpha* species were then inferred using three outgroup combinations. Basal and terminal nodes were reasonably resolved and supported, but a low proportion of non-wing pattern characters resulted in weak resolution and support in the middle of the tree. The most basal members of *Adelpha* feed on the temperate or montane plant family Caprifoliaceae, suggesting that a switch from this family early in the evolutionary history was important in subsequent diversification into tropical lowland habitats. The cladograms confirm suspicions of earlier authors that dorsal mimetic wing patterns have convergently evolved a number of times in *Adelpha*. The subtribal classification of Limenitidini is discussed and both *Lebadea* (from Parthenina) and *Neptina* are transferred to Limenitidina, whereas *Cymothoe*, *Bhagadatta* and *Pseudoneptis* (all formerly Limenitidina) are regarded as *incertae sedis*.

Introduction

Butterflies provide a rich source of material for many topics in evolutionary biology, and the development of computer-based cladistic analysis in recent decades has provided a much firmer foundation for such studies. Phylogenetic work on butterflies has illuminated subjects as diverse as ecological modes of speciation (e.g. Turner, 1976), evolutionary shifts in host-plant and chemical ecology (e.g. Brown *et al.*, 1991; Wahlberg, 2001), chemical communication (e.g. Schulz *et al.*, 1993), and Amazonian (e.g. Brower, 1996; Hall & Harvey, 2002), Gondwanan (e.g. Parsons, 1996) and Andean (e.g. Willmott *et al.*, 2001) biogeography.

Adelpha is the only Neotropical member of tribe Limenitidini, and is one of the largest Neotropical nymphalid genera, with eighty-five species distributed from far north-

western U.S.A. to Uruguay (Willmott, 2003). All species occur in forest habitats, from sea level to over 3000 m. Diversity peaks at the base of the eastern Andes, where local faunas may include up to thirty-nine species (Willmott, 2003), certainly the highest community species richness for any Neotropical nymphalid genus. The dorsal wing surface is typically arrayed with very simple but bright colours, and although a significant number of species have been described only recently (DeVries & Chacón, 1982; Willmott & Hall, 1995, 1999; Austin & Jasinski, 1999; Willmott, 2003), many other species are common and therefore highly conspicuous forest butterflies. The immature stages are diverse in morphology, behaviour and food-plant specialization (Aiello, 1984; Willmott, 2003), and the genus thus offers great promise for evolutionary study. However, such study has been hindered by a chaotic nomenclature and poor understanding of species limits and identification, now addressed in a revision of the genus (Willmott, 2003), and the absence of any phylogenetic hypothesis to date.

Correspondence: Keith R. Willmott, Department of Entomology, The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. E-mail: keiw@nhm.ac.uk

Perhaps the first attempt to define relationships between *Adelpha* species was that of Godman & Salvin (1884), who arranged the known Central American species in a dichotomous key. Although apparently the first to have studied the male genitalia, they still relied mainly on characters of the eyes and dorsal wing pattern. Their arrangement was presumably designed to aid identification rather than to indicate evolutionary relationships, but it had a great influence on all subsequent authors and the curation of most museum collections.

Fruhstorfer (1915), in the first major review of the entire genus, largely followed Godman & Salvin's (1884) order of species, and also made some use of male genitalia and forewing venation. Nevertheless, greatest weight was still placed on characters of the dorsal wing pattern.

Moss (1933) first drew attention to the possibility that the dorsal wing pattern might be a poor indicator of phylogeny, with his study of the immature stages of eleven Brazilian species. Aiello (1984) expanded on this theme and collated all published information on *Adelpha* life histories to attempt to define more 'natural' species groups. She studied eighteen species and recognized seven species groups, providing a key to their identification, but did not intend this to represent cladistic relationships. The remaining sixty-seven species in the genus were omitted from the classification. Otero & Aiello (1996) subsequently suggested that a new, eighth, species group might be required for *A. alala*, and five additional species of which the life histories were unknown were also listed as possible members.

The continually increasing body of knowledge on immature stage morphology suggests deep flaws in the higher-level taxonomic arrangements of earlier authors, however ill-defined, and Aiello (1984) and Otero & Aiello (1996) suggested that the genus might even prove to be paraphyletic with respect to certain Asian limenitidines. In addition, species-level taxonomic study reveals substantial racial variation in the dorsal wing pattern (Willmott, 2003), suggesting that a classification based almost exclusively on such a character set is unlikely to reflect accurately phylogenetic patterns. Indeed, a number of conspecific taxa were implicitly included in different 'species groups' by Fruhstorfer (1915) and other authors (see Willmott, 2003). This study therefore had several goals: to test the value of different character sources in providing phylogenetic information, both within *Adelpha* and within Limenitidini; to test the monophyly of *Adelpha*; and to provide the first comprehensive phylogenetic hypothesis for the genus.

Methods

Analytical approach

The two main goals of this study, testing the monophyly of *Adelpha* and producing a hypothesis of species relationships, were best accomplished using a two-stage approach: a higher-level analysis including a number of outgroup taxa and representative *Adelpha* species, and a lower-level ana-

lysis including fewer outgroup taxa, selected following the results of the first analysis, all *Adelpha* species, and additional characters. This permitted the inclusion of additional characters in the species-level analysis that otherwise vary too much to allow coding, and reduced the likelihood of mistaken homology assessment of characters in distantly related taxa.

Study taxa and outgroup choice

Higher-level analysis. The selection of which species (outside *Adelpha*) to include in the higher-level analysis (and therefore as potential outgroup species for the lower level) was the most complex aspect of this study. *Adelpha* is a member of Limenitidini, a tribe currently placed in the para- or polyphyletic subfamily Biblidinae (Brower, 2000). Limenitidini is therefore equally likely to be the sister group to any of several other nymphalid subfamilies (Harvey, 1991; Brower, 2000). Limenitidini, as treated here, has been recognized by all modern authors (Chermock, 1950; Eliot, 1978; Harvey, 1991), but the principal evidence for its monophyly still remains the structure of the eggs: in all known species these are composed of polygonal, sunken facets, and in almost all known species there are short, hairlike projections at the vertices (Harvey, 1991; Igarashi & Fukuda, 1997, 2000). These projections may be chorionic sculpturing or aeropylar tubes, as suggested by Amiet (2000a). Exceptions include several species of *Pseudacraea* Westwood (Amiet, 2000b), *Pseudoneptis bugandensis* Stoneham and at least one species of *Neptis* Fabricius and *Catuna* Kirby (Amiet, 2002), which lack these fine projections. Chermock (1950) and Harvey (1991) defined the tribe on the basis of a single character, the preservation of the first anal vein (1A) as a short spur at the base of the forewing cubital vein. However, this vein is not present in *Neptis* and its relatives (Chermock, 1950), and also occurs in certain members of Heliconiinae, as noted by Michener (1942) and Brown & Heineman (1972), including the genera *Philaethria* Billberg, *Dryas* Hübner and *Dryadula* Michener (C. Penz, personal communication). Indeed, it is possible that Limenitidini are closely related to Heliconiinae (Brower, 2000). One behavioural trait characteristic of the tribe is the habit of resting with the wings open, and the distinctive, gliding flight with the wings pointed downwards (Eliot, 1978; personal observation). Finally, recent trees generated by cladistic analysis of equally weighted molecular characters also supported monophyly of the tribe, although the most parsimonious tree (MPT) after successive approximations character weighting (SACW) did not (Brower, 2000). Nevertheless, I conclude that monophyly of Limenitidini is sufficiently well supported to assume that the closest relatives of *Adelpha* lie within the tribe. I therefore examined the wing patterns of the majority of species in all Limenitidini genera in museum collections (Allyn Museum of Entomology, Sarasota, FL (AME); The Natural History Museum, London (BMNH); National Museum of Natural History, Smithsonian Institution,

Washington, DC (USNM)), major faunistic works and field guides, including D'Abrera (1985, 1993), Larsen (1991), Corbet & Pendlebury (1992) and Chou (1994, 1998). Dissections were made of males (initially, due to the availability of material) of phenotypically distinctive species from all four previously recognized tribes of Limenitidini: Parthenina, Euthaliina, Neptina and Limenitidina (Harvey, 1991; from hereon subtribes are as defined in the Discussion, unless otherwise specified). Because the primary aim was to choose outgroup species for the analysis of *Adelpha*, rather than to revise the subtribal classification, type species for genera were not necessarily selected. I concentrated in particular on a probably monophyletic group of genera treated by Chermock (1950) as a single genus, *Limenitis* Fabricius (including *Adelpha*) (see Discussion). Genitalic illustrations for many more species were also examined in publications, particularly Chermock (1950), Eliot (1969, 1978) and Chou (1998).

Forty-six non-*Adelpha* species were dissected, including males of thirty-eight species and females of thirty-four species, representing Parthenina (one genus, one species), Euthaliina (five genera, six species), Limenitidina (thirteen genera, thirty-seven species) and *incertae sedis* (two genera, two species) (Table 1). Ultimately, twenty species (one Parthenina, one *incertae sedis* and eighteen Limenitidina) were selected from these taxa for the higher-level analysis, representing morphological variation among the potential outgroup species and choosing, where possible, species with known life histories. All North American species of *Basilarchia* Scudder were also included, as the geographically closest relatives of *Adelpha*. No Euthaliina were included because the monophyly of that group seems well supported, and because the rather autapomorphic genitalia, wing pattern and immature stages would have caused unnecessary problems in character coding. The species are listed in Table 1, and figured in D'Abrera (1985, 1993). Generic combinations are, in many cases, arbitrary (see Discussion).

Among *Adelpha*, the twenty-nine species for which immature characters could be coded were chosen as exemplar taxa for the genus in the higher-level analysis. Qualitatively, these species represent most of the morphological variation occurring within the genus (Willmott, 1999), but an additional species whose immature stages are unknown, *A. gelania*, with many apparently plesiomorphic character states and with no obvious close relatives, was also included.

To root the tree, *Parthenos sylvia* and *Bhagadatta austenia* (Parthenina and *incertae sedis*, respectively, see Discussion) were used as outgroup taxa for the remaining eighteen non-*Adelpha* species and thirty *Adelpha* species. Putative synapomorphies for the ingroup include significantly reduced subdorsal scoli on segment A2 of the fifth-instar larva, in comparison with segments T2 and T3, the adoption of a 'front-arched rear-up' larval resting posture, and larval construction of a mass of leaf material or frass, or both, at the base of the feeding support (see Discussion).

Lower-level analysis. The goal of outgroup selection is to locate the taxon, or group of taxa, that shares the greatest

proportion of character states with the ingroup ancestor. In general, taxa more closely related to the ingroup are less likely to have diverged from the character states of the ingroup ancestor (but see Lyons-Weiler *et al.*, 1998). In this study, with a high proportion of characters from the wing pattern, an additional important criterion was to prefer outgroup taxa with wing patterns that are not strongly 'modified'; many of the Limenitidina patterns are mimetic, resulting in the loss and fusion of major elements of the nymphalid wing pattern groundplan (Nijhout, 1991), with the result that many characters cannot be coded. Four species that appeared closely related to *Adelpha* in the higher-level analysis, with relatively unmodified wing patterns, were chosen as potential outgroup taxa for the lower-level analysis: *Parasarpa zayla*, *Parasarpa zulema*, *Sumalia dudu* and *Sumalia daraxa*.

All eighty-five species within *Adelpha* recognized and figured by Willmott (2003) were included in this study. A single species, *A. herbata* Weymer, is known only from the female specimen figured in the original description, the whereabouts of which is unknown. Fortunately, *Adelpha* are not sexually dimorphic in wing pattern and the original description contains a colour painting of both wing surfaces. Although this illustration is detailed and appears to represent an authentic specimen (it shows certain distinctive wing pattern elements occurring in related species), some character states in the basal areas and anal margins of the wing were not visible or not indicated on the illustration, possibly because these areas are often rubbed during the capture and killing of specimens. Certain external morphological characters also could not be coded for this species, but I was able to examine specimens of all other species. Male genitalia were examined for every species, except *A. herbata*, usually of the nominate and other distinctive subspecies. Female genitalia were examined for all except nine species, for which material was unavailable. During revisionary work on *Adelpha*, published and collection sources of information on the immature stages were comprehensively compiled for all species (Willmott, 2003), providing sufficient information to code characters for twenty-eight species. A single additional species could also be coded for one character, based on a description of the pupa by A. Aiello (personal communication).

Characters

Morphological study. Wing patterns were examined in specimens from the entire range of each species (see Willmott, 1999, 2003), except for *A. herbata*, which is known only from the illustration in the original description. All *Adelpha* taxa are illustrated by Willmott (2003), and outgroup species by D'Abrera (1985, 1993). Terminology for elements of the wing pattern follows Willmott & Hall (1999) (Fig. 1). In most cases, where material was available, male genitalia were examined in several specimens of each species. Typically, fewer females were dissected for each species due to the lack of material. Dissections of *Adelpha* are listed in Willmott (2003), whereas those for outgroup taxa, and

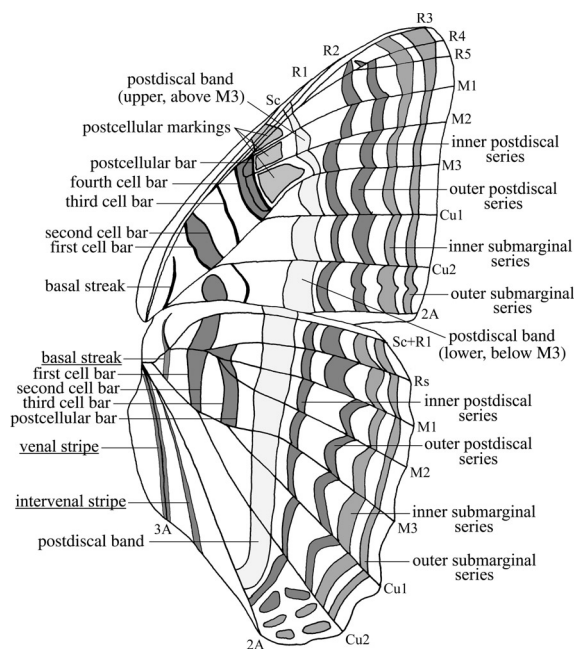


Fig. 1. Elements of the *Adelpha* (and other Limenitidini) wing pattern, with terminology used in this paper. Underlined pattern elements are synapomorphies for *Adelpha*.

several additional *Adelpha*, are listed in Table 1. Wing venation was examined for all species except *A. herbata* and *A. atlantica*, and the morphology of the legs, antennae and labial palpi for representative species from all *Adelpha* species groups (clusters of species with similar genitalia and wing pattern). Because no significant morphological variation in legs, antennae or labial palpi was noted by previous authors (Westwood, 1850; Godman & Salvin, 1884; Fruhstorfer, 1915; Chermock, 1950), these appendages were not examined in non-*Adelpha* species, except for the labial palpi, which showed some variation in colour pattern. Appendages and genitalia were prepared by soaking in hot 10% KOH solution for 15–30 min and subsequently stored in glycerol. All specimens were studied using a Wild M4A stereomicroscope at 30× magnification and drawn using a Wild camera lucida. Terminology for the wing venation follows Comstock & Needham (1918), and to avoid confusion, wing cells are referred to by the veins that bound them. Genitalic terminology follows Klots (1956), except for use of the term ‘clunícula’ (Fruhstorfer, 1915) to refer to the dorsally directed projection on the basal, inner edge of the valva, which is adorned with numerous tiny spines on the inner surface.

Preserved material of various immature stages of a few *Adelpha* species was obtained from individuals (P. DeVries, W. Haber) and public institutions. Such material typically consisted of cast head capsules, larval integuments and

Table 1. Dissections of outgroup taxa examined. Taxa included in the higher-level analysis are marked with an asterisk. Four recent *Adelpha* dissections not included in Willmott (2003) are also listed.

Taxon	Dissections examined
Parthenina Reuter, 1896	
* <i>Parthenos sylvia</i> (Cr.)	1 male: Papua New Guinea, north of Lai (FSCA); 1 female: Malaysia, Perak (BMNH); 1 female: Papua New Guinea, north of Lai (FSCA)
incertae sedis	
* <i>Bhagadatta austenia</i> Mre.	1 male: India, Assam, Margarita (NHM); 1 female: Burma, Sadon (BMNH)
<i>Cymothoe theobene</i> Dbl.	1 male: CAR, Bangui (FSCA); 1 female: CAR, Bangui (FSCA)
Euthaliina Moore, 1895	
<i>Abrota ganga</i> Mre.	1 male: no locality (USNM)
<i>Euptera pluto</i> (Wwd.)	1 male: ‘Zomba, Nyassaland’ (USNM)
<i>Euryphura chalcis</i> F. & F.	1 female: Kenya, Kakamega (KWJH)
<i>Tanaecia godartii</i> (Gray)	1 male: Malaysia, Templer Park (KWJH); 1 female: Malaysia, Cameron Highlands (FSCA)
<i>Tanaecia pelea</i> (Fabr.)	1 male: Malaysia, Bukit Tinggi (KWJH)
Limenitidina Behr, 1864	
* <i>Pseudacraea lucretia</i> (Cr.)	1 male: ‘Africa’ (FSCA); 1 female: Mozambique, Mt Chiluvo (FSCA)
<i>Pseudacraea plutonica</i> Butl.	1 male: Kenya, Kakamega (USNM)
<i>Lasippa tiga</i> (Mre.)	1 male: Malaysia, Templer Park (KWJH)
<i>Neptis duryodana</i> Mre.	1 female: Malaysia, Tai Paiy (FSCA)
* <i>Neptis hylas</i> (Linn.)	1 male: Japan, Hyogo, Mt Masui (FSCA); 1 female: Nepal, Amlekhganj (FSCA); 1 female: Malaysia, Cameron Highlands (FSCA)
<i>Neptis melicerta</i> (Dru.)	1 female: Zimbabwe, Buhera (FSCA)
<i>Neptis nata</i> Mre.	1 male: Malaysia, Kereteka (FSCA)
<i>Neptis saclava</i> Boisdu.	1 female: Tanzania, Manyanara Lake Lodge (FSCA)
<i>Neptis</i> sp.	1 female: Philippines (FSCA)
<i>Auzakia danava</i> (Mre.)	1 male: no locality (USNM)
<i>Tacola larymna</i> (Dbl.)	1 male: Malaysia, Templer Park (KWJH)
<i>Lebadea martha</i> (Fabr.)	1 male: Malaysia, Templer Park (KWJH); 1 female: Vietnam, Pleiku (AME)
* <i>Ladoga camilla</i> (Linn.)	1 male: Japan, Shogunzuka, Tokyo (FSCA); 1 male: France, Env De Rennes

Table 1. Continued.

Taxon	Dissections examined
	(BMNH); 1 female: Hungary (FSCA); 1 female: France, Loiret (FSCA); 1 female: Austria, Leobendorf (FSCA); 1 female: 'Russkein' (FSCA)
* <i>Ladoga reducta</i> (Stdgr.)	1 male: Syria, Afka (USNM); 1 female: France, St Zacharie (FSCA); 1 female: 'Suedtirol' (FSCA)
<i>Ladoga sulphitica</i> (Cr.)	1 male: Taiwan, Nan Chan Shi area, near Puli (FSCA)
<i>Limenitis helmanni</i> Led.	1 male: Russia, Kaymanovka, Ussuriysk (FSCA)
* <i>Limenitis populi</i> (Linn.)	1 male: Japan, Hokkaido (FSCA); 1 female: Czechoslovakia, Cernosice (AME)
<i>Litinga cottini</i> (Ob.)	1 female: China, Ta Tsien-Lou (BMNH)
<i>Litinga mimica</i> (Poujade)	1 female: China, Siao-Lou (BMNH)
* <i>Basilarchia archippus</i> (Cr.)	1 male: U.S.A., Georgia, Wayne Co (FSCA); 1 female: U.S.A., Florida, north Key Largo (FSCA); 1 female: U.S.A., Florida, Gainesville (FSCA)
* <i>Basilarchia arthemis</i> (Dru.)	1 male: U.S.A., Indiana, La Grange Co (FSCA); 1 male: U.S.A., New Hampshire, Andover (FSCA); 1 female: U.S.A., Florida, Gilchrist Co (FSCA)
* <i>Basilarchia lorquini</i> (Bsd.)	1 male: U.S.A., Oregon, Wasco Co (FSCA); 1 female: U.S.A., Oregon, McDonald Forest, Benton Co (FSCA)
* <i>Basilarchia weidemeyerii</i> (W. H. Edw.)	1 male: U.S.A., Utah, Cache Co (FSCA); 1 male: U.S.A., Colorado, no locality (BMNH); 1 female: U.S.A., Colorado, Pinon Mesa, Mesa Co (FSCA)
* <i>Moduza procris</i> (Cr.)	1 male: Malaysia, Templer Park (KWJH); 1 female: India, Darjeeling (AME)
* <i>Moduza lymire</i> (Hew.)	1 male: no locality (USNM); 1 female: Indonesia, Sulawesi (BMNH); 1 female: Indonesia, Sulawesi, Macassar (BMNH)
<i>Pandita sinope</i> Mre.	1 male: Malaysia, Malaca (USNM); 1 female: 'Java?' (AME)
<i>Tarattia lysanias</i> (Hew.)	1 male: Indonesia, 'Celebes' (USNM); 1 female: Indonesia, north Celebes, Tondono (AME); 1 female: Indonesia, Sulawesi, Pic de Bonthain (BMNH)
* <i>Athyma asura</i> Mre.	1 male: China, Ginfu-shan (FSCA); 1 female: Taiwan, Wulai (FSCA)
<i>Athyma cama</i> Mre.	1 female: Malaysia, Cameron Highlands (FSCA); 1 female: Taiwan, Taiping Shan Mtn (FSCA)
<i>Athyma nefte</i> (Cr.)	1 male: Malaysia, Cameron Highlands (KWJH)
* <i>Athyma ranga</i> Mre.	1 male: India, Sikkim (USNM); 1 female: India, Karwar (BMNH)
<i>Athyma reia</i> Mre.	1 male: Malaysia, Kerling (KWJH)
* <i>Athyma selenophora</i> (Koll.)	1 male: Taiwan, Liu Kuei (FSCA); 1 female: Taiwan, Wulai (FSCA); 1 female: Thailand, Pukading (BMNH)
<i>Parasarpa albomaculata</i> Leech	1 male: China, Ningyuenfu (USNM); 1 female: China, Siao Lou (FSCA)
* <i>Parasarpa zayla</i> (Dbld.)	1 male: no locality (USNM); 1 female: Bhutan (BMNH)
* <i>Parasarpa zulema</i> (Dbld.)	1 male: country?, Sinoke (USNM); 1 female: India, Assam (BMNH)
* <i>Sumalia daraxa</i> (Dbld.)	1 male: Thailand, Chiangmai (FSCA); 1 female: India, Sikkim (NHM)
* <i>Sumalia dudu</i> (Wwd.)	1 male: Taiwan, Heng Chun (FSCA); 1 female: India, Assam, Shillong (AME)
<i>Adelpha attica</i>	1 female: Panama, Darién, Cana (USNM)
<i>Adelpha delinita</i>	1 female: Ecuador, Zamora-Chinchi, Río San Francisco (SMS)
<i>Adelpha thesprotia</i>	1 female: French Guiana, Cayenne (NHM)
<i>Adelpha ximena</i>	1 female: Guyana, Coldm Gdns (NHM)

AME, Allyn Museum of Entomology, Sarasota, U.S.A.; FSCA, Florida State Collection of Arthropods, University of Florida, Gainesville, U.S.A.; KWJH, Keith R. Willmott and Jason P. W. Hall collection, U.K.; BMNH, The Natural History Museum, London, U.K.; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; USNM, National Museum of Natural History, Smithsonian Institution, Washington, U.S.A.

pupal cases, and in a very few cases, dried larvae. Dried material of a number of non-*Adelpha* species was also available at the BMNH, and H. Kons loaned larvae and a pupa of *Basilarchia arthemis* in alcohol. Study was restricted to the fifth-instar larva and pupa because of the unavailability of material, and morphology was studied using the same microscope as for adult material. Colour slides and black and white photographs of the immature stages of several *Adelpha* species were provided by J. Mallet, A. Muysshondt and R. Boender, and published illustrations and sketches were also examined. Sources of information on early stages of *Adelpha* taxa are listed in Willmott (2003), and those for non-*Adelpha* taxa are listed in Table 2.

Character coding. The majority of the characters coded (73%) were from the wing pattern, and several particular problems common to all morphological analyses were more prevalent. Wing pattern elements follow a generalized 'groundplan' that can be recognized in all nymphalid butterflies (Schwanwitsch, 1924; Nijhout, 1991), but in many cases certain elements are fused or lost, presenting potential problems in homology assessment. Two principal methods were used to establish homology: the position of pattern elements on the wing, with respect to wing venation, and the use of morphoclines, or the examination of related series of species showing transitional stages. Both methods are also used in the study of structural morphology. In *Limenitidini*,

Table 2. Sources of information on immature stages of outgroup taxa.

Species	Source
<i>Parthenos sylvia</i>	Igarashi & Fukuda (2000: plate 183)
<i>Bhagadatta austenia</i>	Igarashi & Fukuda (2000: plate 185)
<i>Pseudacraea lucretia</i>	Amiet (2000b); NHM
<i>Neptis hylas</i>	Igarashi & Fukuda (1997: plate 174); NHM
<i>Ladoga reducta</i>	Boudinot (1986)
<i>Ladoga camilla</i>	Boudinot (1988); NHM
<i>Limenitis populi</i>	Boudinot (1987); NHM
<i>Basilarchia archippus</i>	Allen (1997); NHM
<i>Basilarchia arthemis</i>	Allen (1997); H. Kongs; NHM
<i>Basilarchia lorquini</i>	Dyar (1891); Comstock (1927)
<i>Basilarchia weidermeyeri</i>	Edwards (1892)
<i>Modusa procris</i>	Morrell (1954), Igarashi & Fukuda (2000: plate 179)
<i>Athyma selenophora</i>	Igarashi & Fukuda (2000: plate 194)
<i>Athyma ranga</i>	Bascombe <i>et al.</i> (1999)
<i>Athyma asura</i>	Igarashi & Fukuda (2000: plate 185)
<i>Sumalia dudu</i>	Igarashi & Fukuda (2000: plate 177)

NHM, The Natural History Museum, London, U.K.

the postdiscal series (see Fig. 1), one of the most phylogenetically informative pattern elements, can usually be traced by examination of the apex and tornus of both wings. In *Adelpha*, the most visually obvious pattern consists of pale markings, strictly 'background' in terms of the nymphalid groundplan (Nijhout, 1991). As these parts of the pattern provided the most phylogenetic information, a different terminology was used for clarity (Willmott & Hall, 1999; Fig. 1), and 'wing pattern element' in this paper typically refers to these pale markings.

A second problem concerns the distinction between genealogical homology and anatomical homology. Homologous pattern elements may be expressed in a similar way, but if there are more subtle and consistent differences between species, suggesting independent origin, I coded distinct character states. However, in the majority of cases, due to the structural simplicity of wing pattern elements, fine-scale differences between species in apparently similar character states are rarely apparent.

A third problem was whether to code homologous pattern elements in different cells as a single character or multiple characters. For example, the postdiscal series on the ventral forewing are variably fused throughout the wing of *Adelpha*, and often provide critical characters distinguishing species. In many cases, the fusion of pattern elements in adjacent cells is independent, especially in the middle of the wing, but towards the apex elements tend to be fused in all cells or none. Thus, the fusion of pattern elements may be treated as independent characters for each cell in some parts of the wing, and as a single character embracing several adjacent cells in other parts. Characters based on colour are particularly subject to this problem; the white or orange coloration on the forewing seems to be strictly dimorphic in some species, affecting numerous cells simultaneously, and variable at the level of individual cells in others.

Fourth, virtually all *Adelpha* and many other Limenitidini are mimetic (Willmott, 2003). Many *Adelpha*, like better known mimetic groups such as *Heliconius* Kluk (e.g. Turner, 1976), thus show significant racial variation in wing pattern, with the result that, in some cases, characters were coded as polymorphic.

Finally, because of the plasticity of the wing pattern, there was an unusually high proportion of characters based on pattern elements that are absent in some species, resulting in hierarchical coding which left many character states equivocal. This problem was partially alleviated by selecting outgroup taxa, where possible, that did not show substantially modified wing patterns from which many elements were lost.

Computer analysis. Two separate sets of analyses were conducted: higher-level, using thirty *Adelpha* and twenty other Limenitidini, rooted with *Bhagadatta austenia* and *Parthenos sylvia*; and lower-level, using eighty-five *Adelpha* and one of three pairs of outgroup taxa: *Sumalia dudu* + *Parasarpa zayla*, *Sumalia dudu* + *Sumalia daraxa*, or *Sumalia dudu* + *Parasarpa zulema*. Table 3 contains a summary of all search routine parameters.

The higher-level analysis was conducted using PAUP* 4.0b10 (Swofford, 1998). Initial searches in the lower-level analysis were performed using both PAUP and NONA 1.6 (Goloboff, 1993). NONA was not used for the higher-level analysis because characters with more than ten states are not accepted. Subsequent searches exploring the effects of character sets and outgroups on tree topology, bootstrapping and obtaining decay indices, were performed with PAUP, which is available on the BMNH computer cluster (see below), and due to ease of operation, as both programmes recovered similar consensus trees (see Discussion) in the initial search.

Maximum parsimony was the optimality criterion for all searches, which were heuristic with tree-bisection-reconnection (TBR) branch swapping. Searches with PAUP were all performed using a two-stage process to reduce the problem of tree islands and to obtain the most robust consensus trees in minimal time, mimicking the 'heuristic search' implemented by NONA: starting trees were obtained by stepwise addition using a random addition sequence and a number of replicate searches were conducted, retaining only a small number of trees (two to five) in each search. The shortest trees were then used as the starting trees for a single search, with the maximum number of trees set at 1000–100 000 according to the matrix and time constraints (searches that reached the latter maximum took approximately 20–30 h to perform). The heuristic search option was also used with NONA, with 1000 replicate searches saving two trees per search, followed by a single search starting with the shortest trees from the replicate searches.

All characters were initially unordered and equally weighted. SACW (Farris, 1969) was used to attempt to reduce the number of MPTs and to improve consensus tree resolution. Characters were reweighted based on the maximum value of their consistency index over all the shortest trees recovered by two-step searches as described above.

Table 3. Parameters for search routines.

Search	Analysis	Character weighting	Start trees source	No. search replicates	Maximum trees/replicate
Higher (OG = 2; IG = 48; characters = 81)					
1	Equal weight – initial	Equal	Stepwise addition	2000	5
2	Equal weight – final	Equal	Stored trees from 1	1	100 000
3	Equal weight – bootstrap (500 rep.)	Equal	Stepwise addition	20	2
4	Equal weight – decay initial	Equal	Stepwise addition	200	5
5	Equal weight – decay final	Equal	Stepwise addition	1	1000
6	SACW – initial	Max. ci	Stepwise addition	1000	2
7	SACW – final	Max. ci	Stored trees from 6	1	100 000
8	SACW – bootstrap (500 rep.)	Wts. of SACW	Stepwise addition	20	2
9	SACW – decay initial	Wts. of SACW	Stepwise addition	200	5
10	SACW – decay final	Wts. of SACW	Stepwise addition	1	1000
Lower 1a (OG = 2; IG = 85; characters = 102)					
11	Equal weight – initial	Equal	Stepwise addition	1000	2
12	Equal weight – final	Equal	Stored trees from 11	1	100 000
13	Equal weight – bootstrap (500 rep.)	Equal	Stepwise addition	20	2
14	Equal weight – decay initial	Equal	Stepwise addition	1000	2
15	Equal weight – decay final	Equal	Stored trees from 14	1	1000
16	SACW – initial	Based on ci	Stepwise addition	1000	2
17	SACW – final	Based on ci	Stored trees from 16	1	–
18	SACW – bootstrap (500 rep.)	Wts. of SACW	Stepwise addition	20	2
19	SACW – decay initial	Wts. of SACW	Stepwise addition	200	5
20	SACW – decay final	Wts. of SACW	Stored trees from 19	1	1000
Lower 1b (OG = 2; IG = 85; characters = 95, immature stage characters omitted)					
21	Equal weight – initial	Equal	Stepwise addition	1000	2
22	Equal weight – final	Equal	Stored trees from 21	1	100 000
23	SACW – initial	Based on ci	Stepwise addition	1000	2
24	SACW – final	Based on ci	Stored trees from 23	1	–
Lower 2 (OG = 2; IG = 85; characters = 102)					
25	Equal weight – initial	Equal	Stepwise addition	1000	2
26	Equal weight – final	Equal	Stored trees from 25	1	100 000
27	SACW – initial	Based on ci	Stepwise addition	1000	2
28	SACW – final	Based on ci	Stored trees from 27	1	–
Lower 3a (OG = 2; IG = 85; characters = 102)					
29	Equal weight – initial	Equal	Stepwise addition	1000	2
30	Equal weight – final	Equal	Stored trees from 29	1	100 000
31	SACW – initial	Based on ci	Stepwise addition	1000	2
32	SACW – final	Based on ci	Stored trees from 31	1	–
Lower 3b (OG = 2; IG = 84; characters = 102)					
33	Equal weight – initial	Equal	Stepwise addition	1000	2
34	Equal weight – final	Equal	Stored trees from 33	1	100 000
35	SACW – initial	Based on ci	Stepwise addition	1000	2
36	SACW – final	Based on ci	Stored trees from 35	1	100 000

Outgroups (OG) and ingroups (IG) for searches: Higher: OG – *Bhagadatta austenia* + *Parthenos sylvia*; IG – remaining 'higher-level' taxa; Lower 1a, b: OG – *Parasarpa zayla* + *Sumalia dudu*; IG – *Adelpha*; Lower 2: OG – *Sumalia dudu* + *Sumalia daraxa*; IG – *Adelpha*; Lower 3a: OG – *Parasarpa zulema* + *Sumalia dudu*; IG – *Adelpha*; Lower 3b: OG – *Parasarpa zulema* + *Sumalia dudu*; IG – *Adelpha*, *A. demialba* deleted. SACW, successive approximations character weighting; rep., replicate.

Strict consensus trees are used to summarize shortest tree topologies. To estimate the support for clades based on this character matrix, bootstrapping values (Felsenstein, 1985) and decay indices (Bremer, 1988, 1994), calculated using AUTODECAY 4.0 (Eriksson, 1998), are provided. Five hundred bootstrap replicates were run for each analysis. Each bootstrap replicate was made using starting trees obtained by stepwise addition with twenty random addition

sequences, retaining no more than two trees from each search. Each constrained search used to calculate decay indices included 200–2000 random addition sequence replicates, with a maximum of two to five trees per replicate, followed by a second search, using starting trees saved from the first search, with the maximum number of trees set at 1000 (Table 3). Decay indices for searches with characters reweighted through SACW are rescaled by multiplying by

L_{EW}/L_{SACW} , where L_{EW} is the length of the shortest tree with equally weighted characters, and L_{SACW} is the weight of the shortest tree with SACW (Bremer, 1994).

Larger searches were performed on the computer cluster of the Department of Zoology, BMNH, using eight AMD 900 MHz processors, whereas smaller searches were conducted on a Carrera PC computer with an AMD 600 MHz processor. Trees were examined using WINCLADA version 0.9.9 (Nixon, 1999), in addition to MACCLADE version 3.05 (Maddison & Maddison, 1995). Character changes were optimized on Figs 7, 10 and 11 using ACCTRAN optimization, except for changes on branches leading to two or more clades with different character states, where those states also differed from the sister group. In such cases, PAUP arbitrarily chooses the lower numbered state as the basal change, meaning that optimized changes depend only on the numbering system for character states. To avoid this misleading result, in such cases the appearance of a particular character state is shown on the basal branch of the largest clade that contains only that character state.

Characters

One hundred and fourteen characters (Appendix 1) were coded, including 106 from the adult (body, five; venation, one; wing pattern, eighty-three; male genitalia, twelve; female genitalia, five) and eight from the immature stages (see Appendix 2). Polymorphic character states are separated by '.', and character states that were not coded are indicated by '-'. Of these 114 characters, seventy-six were binary and thirty-eight multistate, and all were unordered. Synapomorphies for larger clades and, where relevant, issues in character coding are discussed in Appendix 1. Character states are illustrated in Figs 2–5.

Results

Tree topology and support, and effect of different outgroup taxa

Higher-level analysis. The higher-level search found eighty-seven MPTs of length 394, consistency index = 0.48 and retention index = 0.73 (Table 4). Two rounds of SACW reduced the number of MPTs to nine (of length 166 and 395, respectively, before and after restoring character weights to one). Strict consensus trees for both equally weighted and SACW analyses are shown in Fig. 6, with bootstrap values over 50 and decay indices. Although the MPTs in the SACW analysis were longer when character weight was restored to unity than those of the equally weighted analysis, there was no topological conflict between the two consensus trees. Figure 7 illustrates character changes along each branch of the SACW consensus tree.

The ingroup was found to be monophyletic only in the SACW consensus tree, with only weak support. The Asian *Neptis hylas* and African *Pseudacraea lucretia* appear as sister

taxa, although again this is weakly supported, and these two form the sister clade to the remaining ingroup species. Consensus trees from both equally weighted and SACW analyses place the North American species of *Basilarchia* as a strongly supported clade. The SACW analysis also places *Basilarchia* close to the European *Ladoga camilla*, *Ladoga reducta* and *Limentities populi*, with these seven Holarctic representatives basal to all remaining species.

Among the remaining non-*Adelpha* species, both equally weighted and SACW trees contain a clade corresponding to *Athyma (sensu lato)*, which is well supported. Relationships between the six remaining non-*Adelpha* species, in *Moduza Moore*, *Parasarpa Moore* and *Sumalia Moore*, were unresolved in the equally weighted analysis, but the SACW analysis placed them as the closest relatives to *Adelpha*, with *Sumalia dudu* as sister group to *Adelpha*. However, branch support for these relationships is weak.

Both equally weighted and SACW trees contain *Adelpha* as a well supported monophyletic group, with the inclusion of *A. bredowii*. Strongly supported clades within *Adelpha* include the *alala*-group, the *serpa*-group (including *A. bredowii*, the most strongly supported clade in the analysis), more derived members of the *serpa*-group, and the sister taxa *A. mesentina* and *A. lycorias* (see Fig. 8 for species group definitions). Less strongly supported clades that were nevertheless evident in both equally weighted and SACW consensus trees include the *phylaca*-group and the *cocala*-group. Although relationships between the *serpa*-group, the *alala*-group and remaining *Adelpha* are only weakly resolved, both equally weighted and SACW consensus trees found the *alala*-group to be the most basal, the sister clade to all other *Adelpha*.

Lower-level analyses. In the first lower-level analysis, with *Parasarpa zayla* and *Sumalia dudu* as outgroup, both PAUP and NONA found MPTs of the same length (563 in PAUP, 475 in NONA, due to steps within terminals not being counted in NONA). The PAUP search was terminated at 100 000 trees (Table 4), and the NONA search was terminated at 63 500 trees, once it became apparent that MPTs found by both were of the same length. The PAUP consensus tree differed from that in NONA only in the collapse of several additional nodes. All further discussion is confined to the results obtained using PAUP.

Despite poor resolution, the overall structure of the consensus tree (Fig. 8) is similar to that of the higher-level analysis, with the *alala*-group basal to the remaining *Adelpha*. The *serpa*-group is strongly supported, with *A. bredowii* the most basal species, and *A. gelania* the sister taxon (only weakly supported). *Adelpha fessonia* is the sister species to the other *Adelpha*. Among the other *Adelpha*, several clades were recovered that were also apparent in the higher-level analysis, including *syma* + *viola* + *cytherea* + *salmonaeus* and the *phylaca*-group.

The second and third equally weighted analyses (Table 4), with *Sumalia dudu* + *Sumalia daraxa* and *Sumalia dudu* + *Parasarpa zulema* as outgroups, respectively, produced consensus trees with even less resolution, collapsing the nodes marked with black circles in Fig. 8. The third

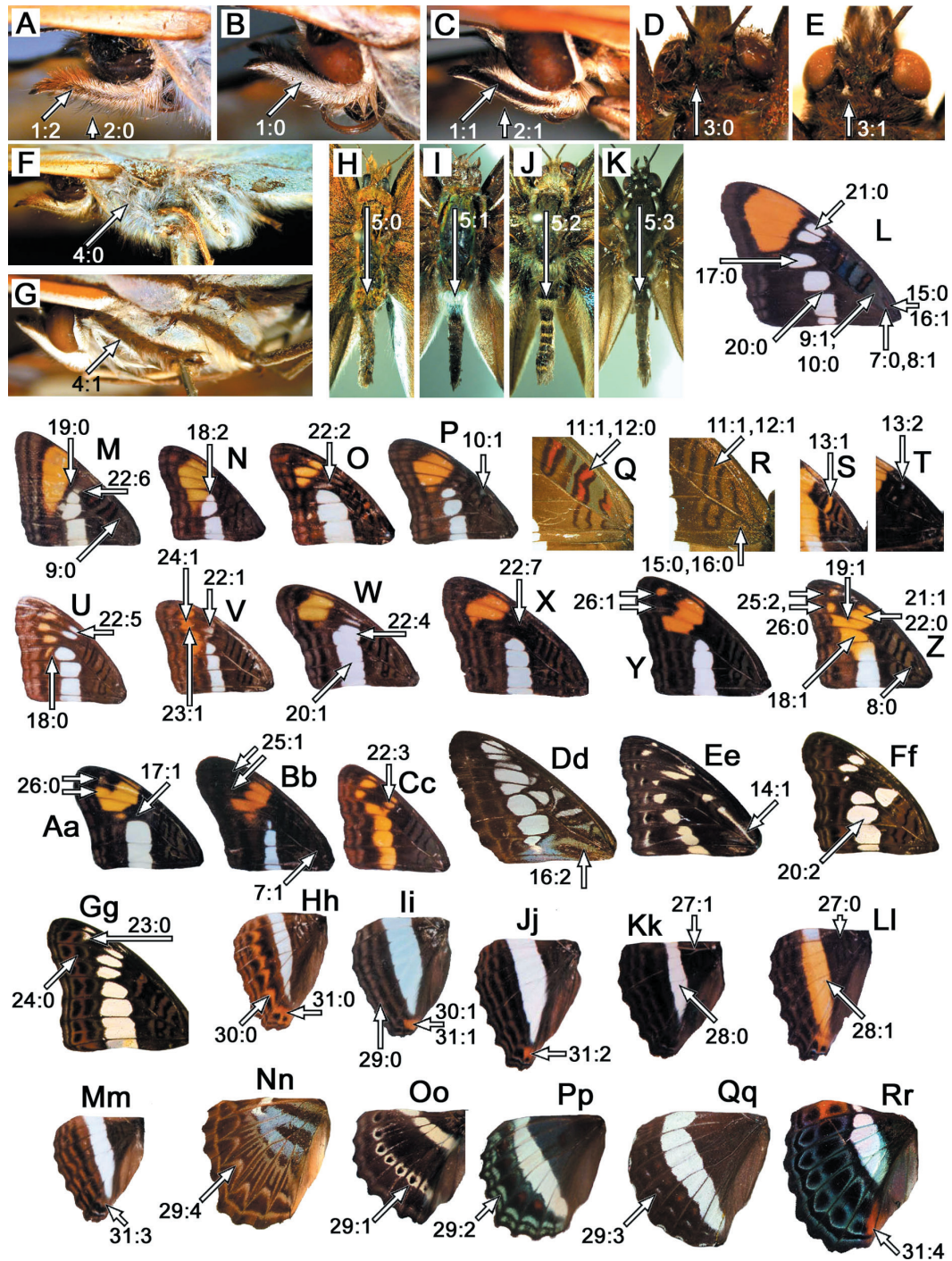


Fig. 2. Body and dorsal wing patterns of *Adelpha* and outgroup species, illustrating characters 1–5, 7–31. Lateral (A–C) and dorsal (D–E) views of the head; lateral (F, G) and dorsal (H–K) views of the body; forewing (L–Gg), hindwing (Hh–Rr). All taxa are *Adelpha* unless stated otherwise. A, *Parasarpa zayla* (Sikkim, India); B, *A. alala negra*; C, *A. mesentina*; D, *A. alala negra*; E, *A. bredowii eulalia*; F, *Parasarpa zayla*; G, *A. bredowii eulalia*; H, *Parasarpa zayla*; I, *Athyma asura* (Assam, India); J, *Parthenos sylvia* (Perak, Malaysia); K, *Pseudacraea lucretia* (Ethiopia); L, *A. bredowii eulalia*; M, *A. diocles creton*; N, *A. zea*; O, *A. paraena reyi*; P, *A. serpa serpa*; Q, *A. gelania arecosa*; R, *A. iphichus iphichus*; S, *A. heraclea makkeda*; T, *A. lycorias melanthe*; U, *A. alala negra*; V, *A. corcyra corcyra*; W, *A. basiloides*; X, *A. iphichus iphichus*; Y, *A. naxia naxia*; Z, *A. capucinus capucinus*; Aa, *A. barnesia*; Bb, *A. felderi*; Cc, *A. olynthia*; Dd, *Parthenos sylvia*; Ee, *Athyma asura*; Ff, *Moduza procris* (Malacca, Malaysia); Gg, *Parasarpa zulema* (Assam, India); Hh, *A. corcyra corcyra*; Ii, *A. serpa diadochus*; Jj, *A. barnesia leucas*; Kk, *A. pollina*; Ll, *A. leuceria leuceria*; Mm, *A. cocala cocala*; Nn, *Parthenos sylvia*; Oo, *Athyma asura*; Pp, *Basilarchia arthemis* (Canada); Qq, *Basilarchia weidermeyerii* (U.S.A.); Rr, *Moduza lymire* (Sulawesi, Indonesia).



Fig. 3. Ventral wing patterns of *Adelpha* and outgroup species, illustrating characters 32–89. Forewing (A–X), hindwing (Y–Xx). All taxa are *Adelpha* unless stated otherwise. A, *A. alata negra*; B, *A. bredowii eulalia*; C, *A. nea nea*; D, *A. serpa diadochus*; E, *A. seriphia godmani*; F, *A. seriphia pione*; G, *A. plesaura phliassa*; H, *A. iphicleola gortyna*; I, *A. melona leucocoma*; J, *A. epione agilla*; K, *A. cytherea aea*; L, *A. viola pseudococala*; M, *A. capucinus capucinus*; N, *A. mesentina*; O, *A. attica attica*; P, *A. boreas boreas*; Q, *A. saundersii saundersii*; R, *A. argentea*; S, *A. jordani*; T, *Parthenos sylvia*; U, *Athyma asura*; V, *Basilarchia weidermeyer* (Colorado, U.S.A.); W, *Ladoga camilla* (Rennes, France); X, *Sumalia dudu* (Assam, India); Y, *A. alata negra*; Z, *A. bredowii californica*; Aa, *A. diocles diocles*; Bb, *A. bredowii eulalia*; Cc, *A. serpa diadochus*; Dd, *A. fessonia fessonia*; Ee, *A. mythra*; Ff, *A. iphichus iphichus*; Gg, *A. melona leucocoma*; Hh, *A. delinita delinita*; Ii, *A. erotia erotia*; Jj, *A. mesentina*; Kk, *A. cocala cocala*; Ll, *A. irmina tumida*; Mm, *A. lamasi*; Nn, *A. saundersii saundersii*; Oo, *A. argentea*; Pp, *Parasarpa zayla*; Qq, *Limenitis populi* (France); Rr, *Athyma selenophora* (Thailand); Ss, *Neptis hylas* (Malaysia); Tt, *Pseudacraea lucretia*; Uu, *Basilarchia archippus* (California, U.S.A.); Vv, *Basilarchia arthemis*; Ww, *Athyma asura*; Xx, *Parthenos sylvia*.

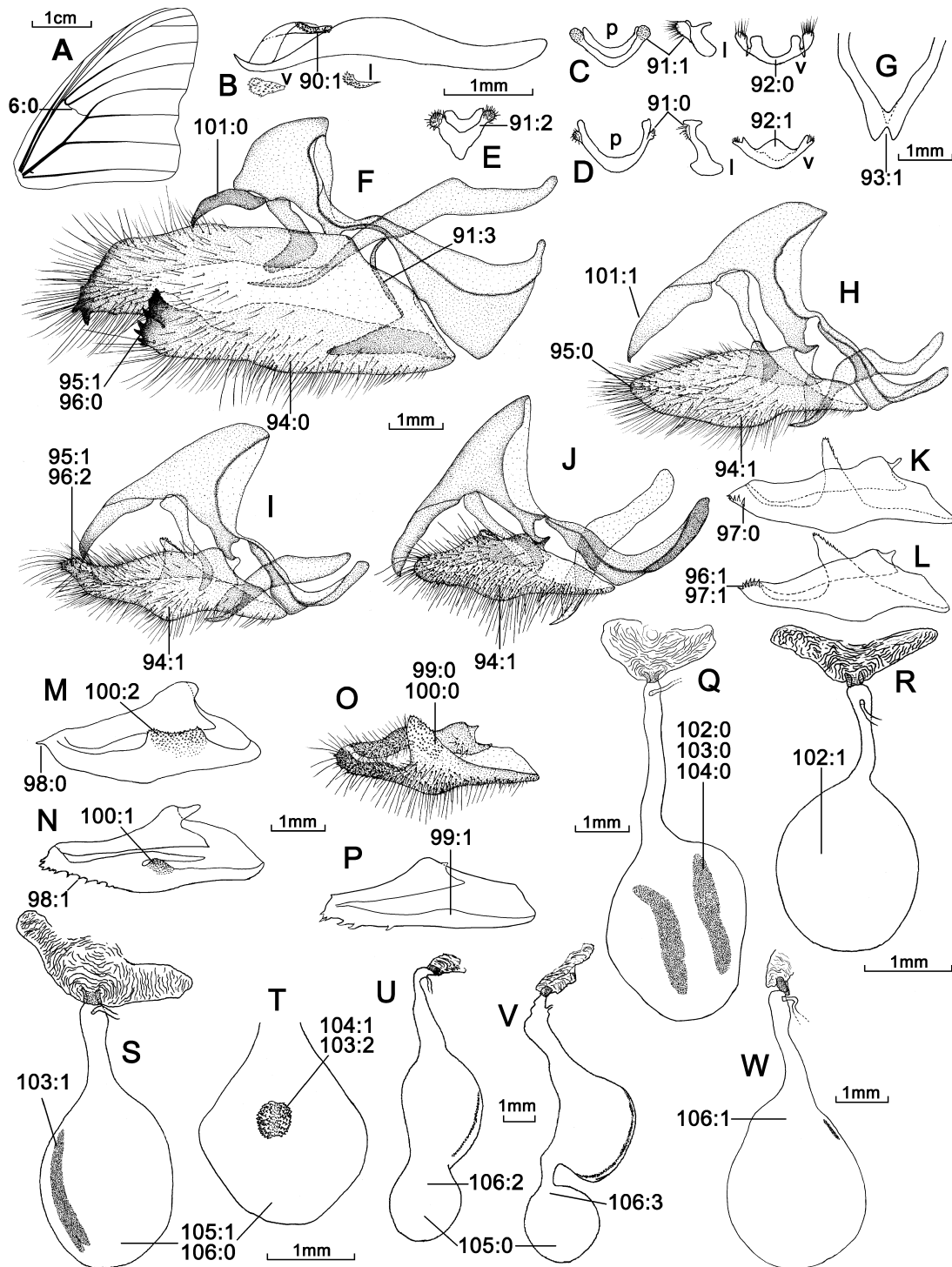


Fig. 4. Venation and genitalia of *Adelpha* and outgroup species, illustrating characters 6, 90–106. All taxa are *Adelpha* unless stated otherwise. A, Forewing venation, *A. serpa*. B, Lateral view of aedeagus, with separate ventral (v) and lateral (l) views of the sclerotized pad on the inside of the vesica, *A. serpa celerio*. C, D, Juxta, posterior (p), lateral (l) and ventral (v) views: C, *A. alala completa*; D, *A. serpa celerio*. E, Juxta, ventral view, *Moduza procris*. F, Male genitalia, lateral view, *Parthenos sylvia*. G, Gnathos, posterior view, *A. diocles creton*. H–J, Male genitalia, lateral view: H, *Parasarpa zayla*; I, *Sumalia dudu*; J, *A. mesentina*. K–P, Lateral view of male genitalic valva, outside (K, L), inside (M–P): K, *A. epione agilla*; L, *A. ipichlus estrecha*; M, *A. pithys*; N, *A. zea*; O, *A. mesentina*; P, *A. bredowii californica*. Q–W, Female genitalia, dorsal (Q–S), ventral (T) and lateral (U–W) views: Q, *A. mesentina*; R, *A. erymanthis erymanthis*; S, *A. malea aethalia*; T, *A. zea*; U, *Limenitis populi*; V, *Basilarchia archippus*; W, *Parasarpa zayla*.

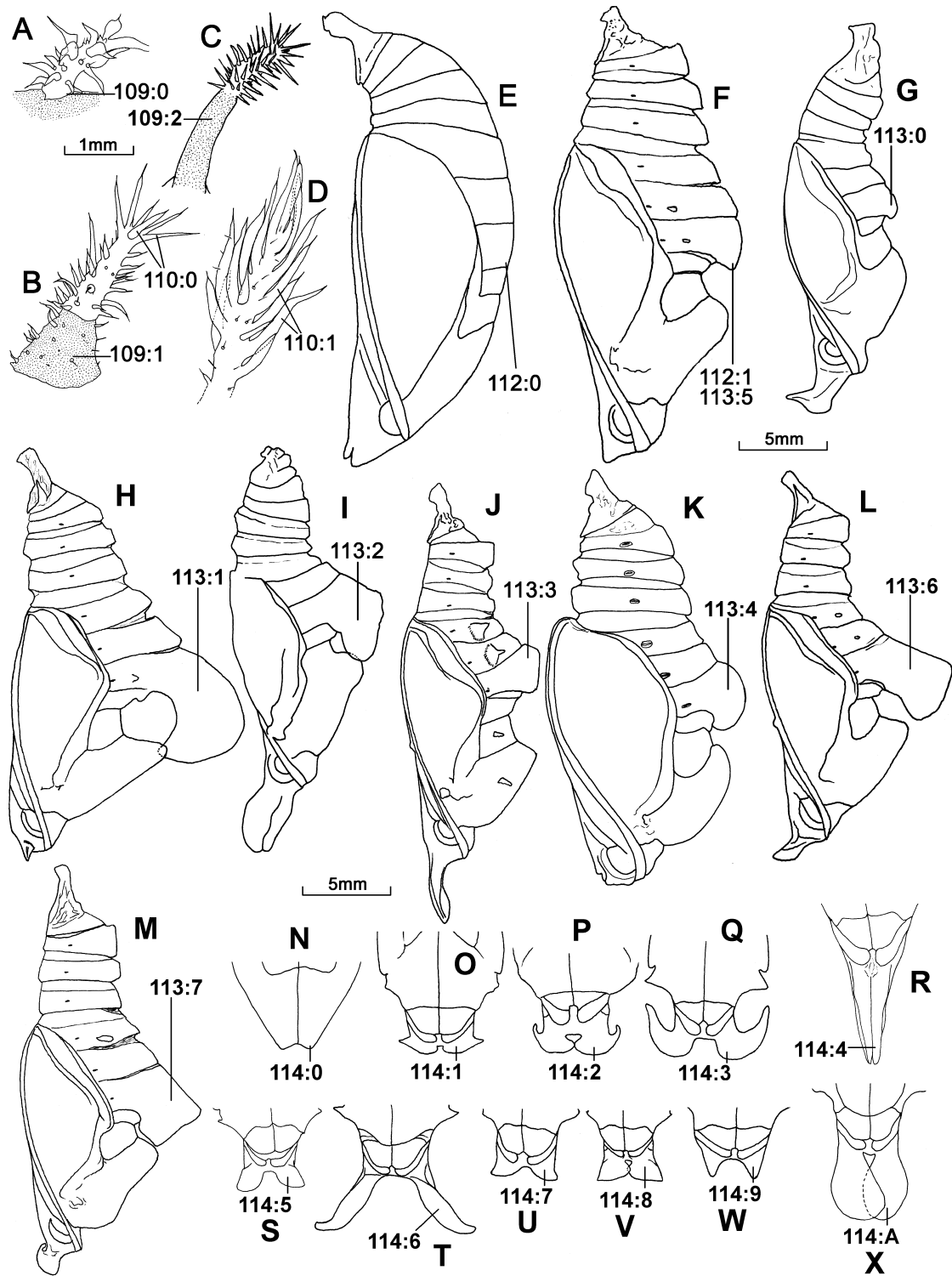


Fig. 5. Immature stage morphology of *Adelpha* and outgroup species, illustrating characters 107–114. All taxa are *Adelpha* unless stated otherwise. A–D, Fifth-instar larval subdorsal scoli on segment A2: A, *A. capucinus capucinus*; B, *A. viola pseudococala*; C, *Sumalia dudu*; D, *A. paraena paraena*. E–M, Pupa, lateral view: E, *Parthenios sylvia*; F, *A. tracta*; G, *Moduza procris*; H, *A. thesprotia*; I, *Sumalia dudu*; J, *A. serpa diadochus*; K, *Limenitis populi*; L, *A. fessonia fessonia*; M, *A. melona leucomoma*. N–X, Pupal cephalic projections, dorsal view: N, *Parthenios sylvia*; O, *A. thesprotia*; P, *A. melona leucomoma*; Q, *A. plesaure phiassa*; R, *Pseudacraea lucretia*; S, *Ladoga camilla*; T, *A. serpa diadochus*; U, *A. tracta*; V, *A. fessonia fessonia*; W, *A. viola pseudococala*; X, *Sumalia dudu*.

Table 4. Tree statistics. All results from PAUP, unless specified.

Search	Analysis	MPT length	Number of MPTs	CI	RI
Higher					
1	Equal weight – initial	394	90		
2	Equal weight – final	394	87	0.48	0.73
6	SACW – initial	166	9		
7	SACW – final	166	9	0.63	0.80
Lower 1a					
11	Equal weight – initial	563	28		
12	Equal weight – final	563	100 000 (preset limit)	0.45	0.74
16	SACW – initial	171	104		
17	SACW – final	171	13 124	0.61	0.84
Lower 1a (NONA)					
11	Equal weight – initial	475*	16		
12	Equal weight – final	475*	63 500	–	–
Lower 1b					
21	Equal weight – initial	520	4		
22	Equal weight – final	520	100 000 (preset limit)	0.43	0.74
23	SACW – initial	139	104		
24	SACW – final	139	115	0.57	0.84
Lower 2					
25	Equal weight – initial	567	20		
26	Equal weight – final	567	100 000 (preset limit)	0.45	0.74
27	SACW – initial	172	66		
28	SACW – final	172	13 139	0.61	0.83
Lower 3a					
29	Equal weight – initial	563	24		
30	Equal weight – final	563	100 000 (preset limit)	0.45	0.74
31	SACW – initial	171	78		
32	SACW – final	171	1604	0.62	0.84
Lower 3b					
33	Equal weight – initial	558	16		
34	Equal weight – final	558	100 000 (preset limit)	0.46	0.75
35	SACW – initial	171	28		
36	SACW – final	171	8060	0.62	0.84

Tree lengths in NONA and PAUP appear to differ markedly because steps within terminals are not counted by NONA. MPT, most parsimonious tree; CI, consistency index, RI, retention index; SACW, successive approximations character weighting.

equally weighted analysis additionally collapsed the nodes marked with white circles in Fig. 8. However, there is no topological conflict among these three consensus trees and all three recovered the majority of smaller clades.

Initial equally weighted searches for the third analysis, terminated at a lower number of trees, suggested that a single divergent species, *A. demialba*, might have strongly influenced the results. The ventral wing pattern of *A. demialba* is similar to many other *Adelpha* that appear as more derived in other analyses. The dorsal forewing pattern, however, is highly autapomorphic, with all pattern elements white, including a number of elements of the submarginal series, that are otherwise never, or almost never, expressed in other *Adelpha*. Given the strong selection on dorsal forewing patterns in all other *Adelpha*, it seems likely that the large white area of *A. demialba* also has adaptive value. The selection for white forewing coloration may thus simultaneously affect coding in a number of characters involving the colour and fusion of pattern elements, as the orange coloration that normally

extends across pattern elements is suppressed. Therefore, the effect of *A. demialba* on tree topology was tested by deleting this species and running the search again (analysis 3b, Tables 3, 4). The resulting equally weighted consensus tree was identical to that of the first analysis (Fig. 8), except for placing *A. mythra* and *A. poltius* as sister species.

SACW in all cases stabilized after two rounds and greatly reduced the number of MPTs, producing significantly more resolved consensus trees. The first and second SACW analyses produced identical consensus trees (Fig. 9). Bootstrap and decay index values are given in Fig. 9, and character changes are illustrated for the first analysis in Figs 10 and 11. The SACW MPTs differ in topology from the equally weighted MPTs, in the first analysis having a length of 569 (compared with 563) when character weights were restored to unity. Notable changes between equally weighted and SACW trees include the reversal of branching order in the *alala*-group and the insertion of *A. pollina* into the *phylacae*-group as sister to *A. thesprotia*.

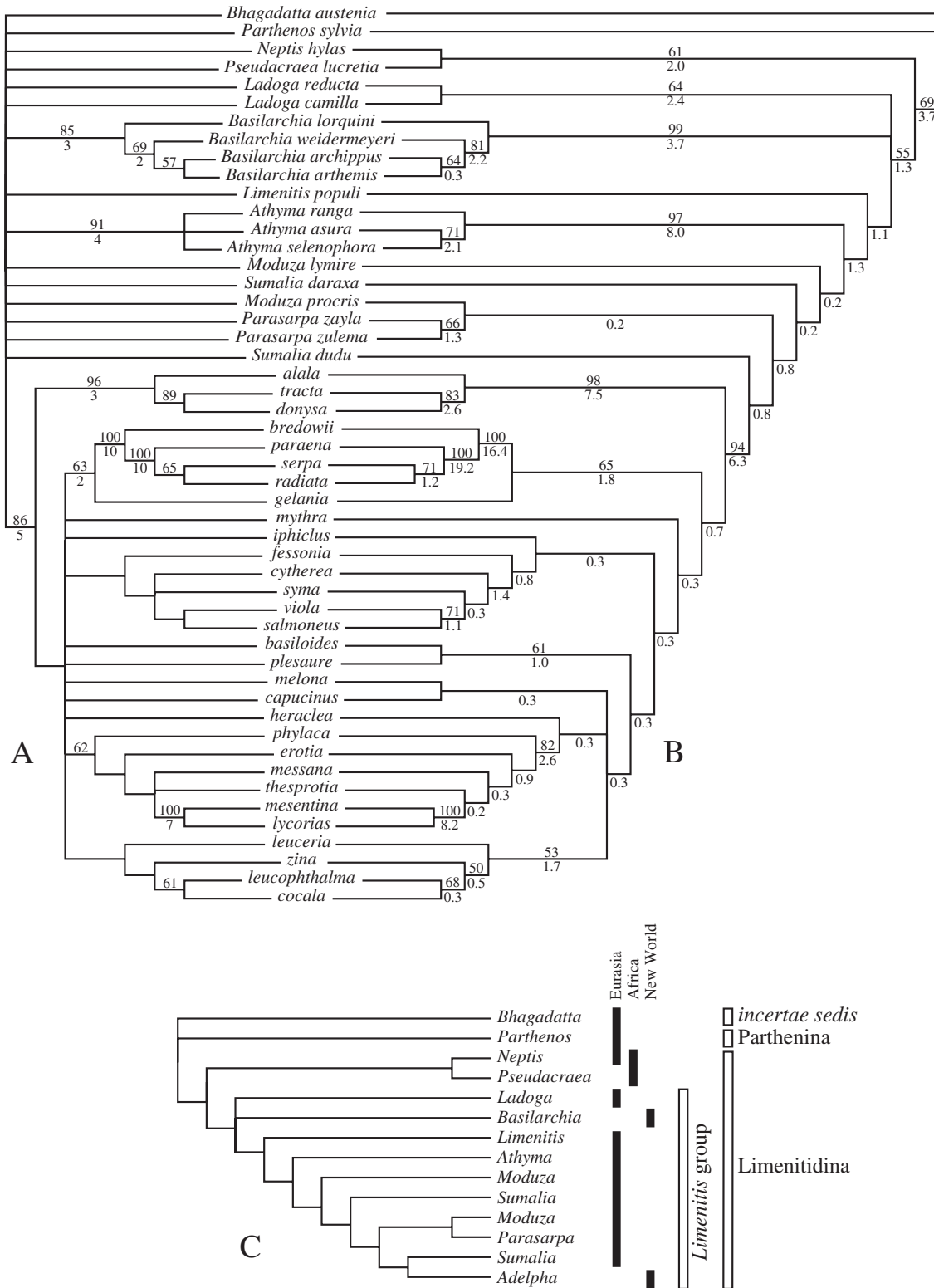


Fig. 6. Cladograms illustrating hypothesized relationships between *Adelpha* and other Limenitidina. Bootstrap values greater than 50 (above branches) and decay indices (below branches) are shown. A, Strict consensus of eighty-seven most parsimonious trees from the equal weighted higher-level analysis; B, strict consensus of nine most parsimonious trees after successive approximations character weighting in the higher-level analysis; C, summary of generic relationships, geographical distribution and classification.

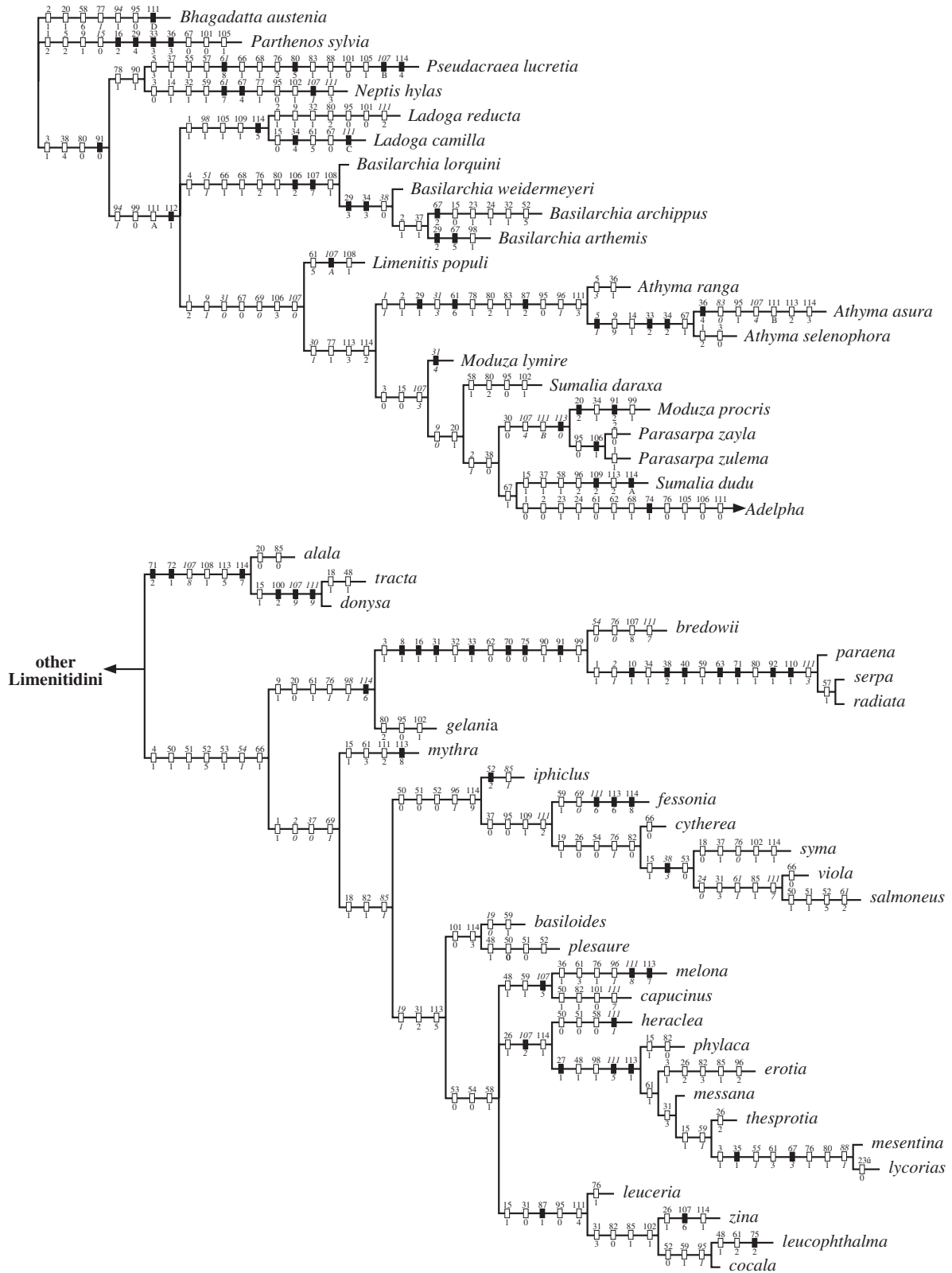


Fig. 7. Strict consensus of nine most parsimonious trees after successive approximations character weighting in the higher-level analysis (same as Fig. 6B), showing character changes (ACCTRAN optimization).

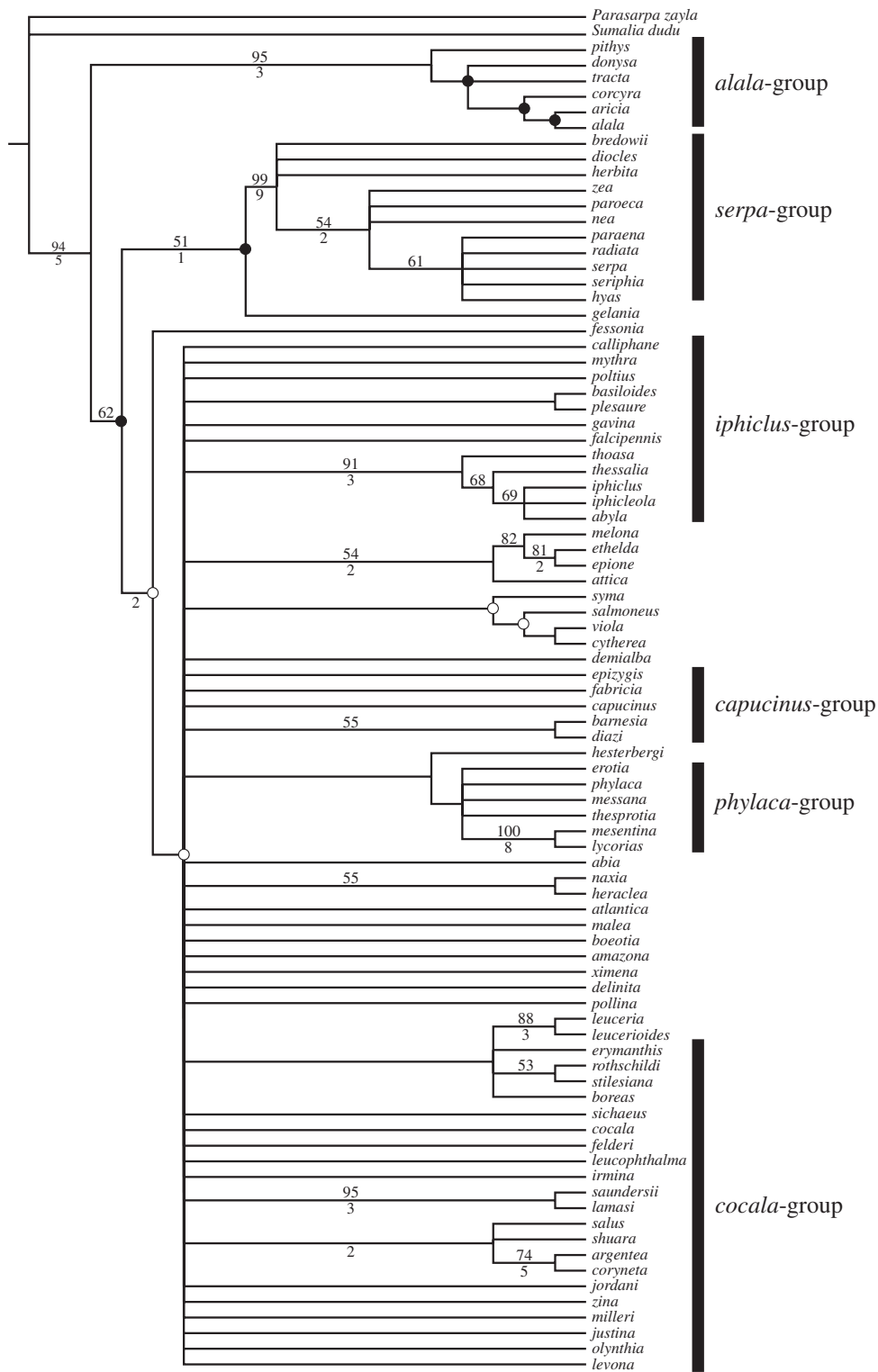


Fig. 8. Cladogram illustrating hypothesized relationships between *Adelpha* species. Strict consensus of 100 000 (preset limit) most parsimonious trees from the equal weighted lower-level analysis, with *Sumalia dudu* and *Parasarpa zayla* as outgroup species (lower-level analysis 1a). Bootstrap values greater than 50 (above branches) and decay indices (below branches) are shown. Nodes collapsed in the strict consensus of trees from lower-level analyses 2 (outgroup *Sumalia dudu*, *Sumalia daraxa*) and 3 (outgroup *Sumalia dudu* and *Parasarpa zulema*) are indicated as black and white circles, respectively. Species groups as recognized in Willmott (2003) are indicated.

The third lower-level analysis, with or without *A. demialba* deleted, produced a rather different SACW consensus tree topology. Major differences include the *serpa*-group shifted to a position immediately basal of *A. demialba*, the clade *syma* + *cytherea* + *viola* + *salmonus* + *epizygis* + *abia* moved to a position immediately after *A. thoasa* and relatives, and *cocala* + *amazona* + *boeotia* moved to become sister clade to *A. jordani*. Clades supported in the SACW consensus trees of all three analyses are marked in bold in Fig. 9.

Effect of different character sets on tree topology

To examine the effect of independent character sets on tree topology, the first analysis (*Parasarpa zayla* + *Sumalia dudu* as outgroup) was repeated with the seven immature characters omitted. Unfortunately, no meaningful analyses could be performed with other possible character partitions alone (e.g. genitalia, immature stages) because of the small number of characters in these partitions. The analysis with adult characters alone (1b) produced a highly resolved consensus tree from both equally weighted and SACW searches (Fig. 12). Immature stage characters, although few in number, thus substantially reduce the resolution in equally weighted consensus trees.

The overall structure of the equally weighted consensus tree (Fig. 12A) is the same as in SACW analyses with all characters (Fig. 9), with the *alala*-group the most basal, followed by *gelania* and the *serpa*-group, then *fessonia* and the other *Adelpha*. Many of the smaller clades evident in the SACW analyses of all characters were also recovered, the notable exception being *syma* + *cytherea* + *viola* + *salmonus*, which occurred as a monophyletic group lacking *salmonus* in the equally weighted search, and as a polyphyletic group in the SACW search.

The SACW consensus tree (Fig. 12B) is similar in most respects to that derived from all characters (Fig. 9), differing most prominently in placing the *iphiclus*-group as monophyletic, rather than paraphyletic, and in its placement of *cocala* + *amazona* + *boeotia*.

Homoplasy and information content of different character sets and different wing areas

Maximum consistency indices for each character and average maximum consistency indices for different character partitions in analysis 1 are given in Appendix 1, with the equally weighted value being followed by the SACW value. The highest average is that for immature stage characters, but this value is strongly affected by the large proportion of unknown character states which resulted in optimization of the character over the tree and thus an artificially high consistency index. The next highest average is that for male genitalia.

Among possible wing pattern partitions, average consistency indices are fairly homogeneous. However, a more uneven pattern emerges when the average consistency

indices of different wing areas are considered (Fig. 13). There is a notable peak in homoplasy in the postdiscal areas of the wings, with the least homoplasious characters occurring in the basal and distalmost areas of the wing.

Discussion

Characters and computer analysis

The most notable aspect of this study is the extreme morphological homogeneity of *Adelpha*, and indeed all limenitidines dissected. This feature of the tribe was noted by Doherty over a century ago: 'one characteristic of what I call Nymphalidae (i.e. the *Neptis*-*Euthalia*-*Limenitis* group) is the entire absence of true genera; the structure is plastic, and one type melts insensibly into another' (in Elwes, 1891: 251). Certainly, Chermock (1950) was similarly frustrated, combining perhaps as many as 200 species into genus *Limenitis* for want of firm morphological characters. The few genitalic characters that were coded here typically define small clades of evidently closely related species, providing no insight at deeper nodes. The result is that 73% of characters in this analysis were derived from the wing pattern, contrasting with, for example, a similar proportion of characters from the abdomen and genitalia in the riordinid butterfly subtribe *Theopeina* (Hall, 2002), and 56% of characters from the genitalia and wing venation in the nymphalid genus *Eunica* Hübner (Jenkins, 1990). The obvious result is that, without such corroborative morphological data, much of the internal topology of resulting trees is at best weakly supported.

Nevertheless, despite the evidently strong selection on dorsal wing pattern through mimicry in *Adelpha* (Willmott, 2003), wing pattern characters still provided significant character information throughout the tree, confirming the value of this character set in cladistic analyses of butterflies (e.g. Nylin *et al.*, 2001; Willmott *et al.*, 2001; Hall, 2002). In *Adelpha*, the forewing colour patterns selected for mimicry lie in the postdiscal area, and this is evident from examination of the variation in homoplasy across the wing (Fig. 13). The basal area of both wings, by contrast, provides characters with typically higher consistency indices, including three synapomorphies for the genus itself (62: 1, 68: 1, 74: 1; Figs 1; 3Y, Z, Gg). One of the two universal synapomorphies for *Theope* Doubleday is also a wing pattern character in the basal area of the ventral forewing (Hall, 2002), and it seems likely that, in general, visually orientated sexual or natural selection on this region of the wing will be lower than more distal regions, simply due to its smaller area and thus visibility.

The three separate lower-level analyses highlight perhaps the most serious potential problem with datasets containing a large proportion of wing pattern characters: the danger of coding homologous pattern elements as independent characters in different wing cells, when such characters in reality exhibit varying degrees of genetic independence. This problem contributes a currently unknown quantity of 'noise' to



Fig. 9. Strict consensus of 13 124 most parsimonious trees after successive approximations character weighting in the lower-level analysis, with *Sumalia dudu* and *Parasarpa zayla* as outgroup species (lower-level analysis 1a). Bootstrap values greater than 50 (above branches) and decay indices (below branches) are shown. Clades in bold are common to all three analyses. Membership of three major mimetic rings is indicated to the right of the cladogram.

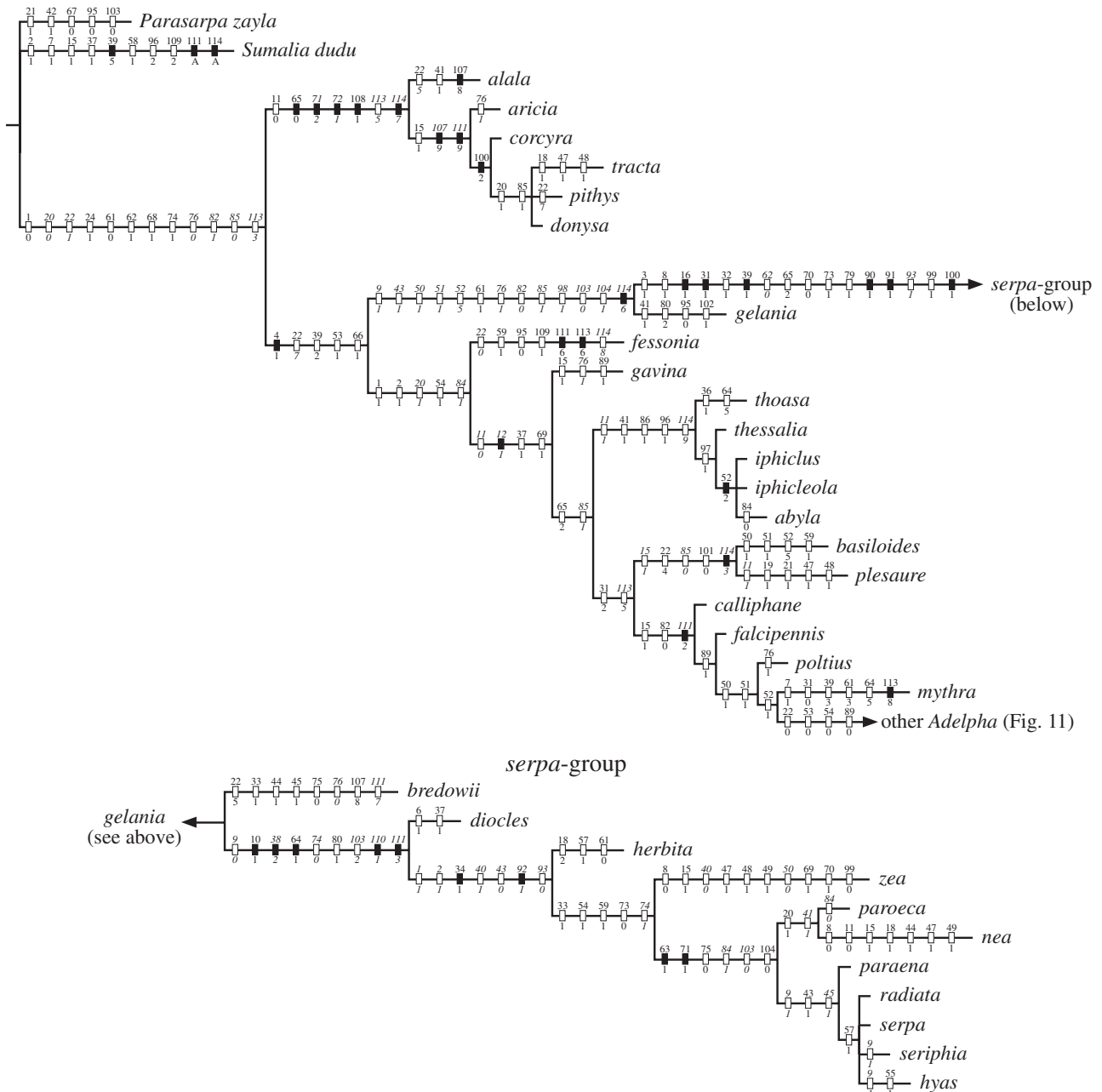


Fig. 10. Upper half of strict consensus of 13 124 most parsimonious trees after successive approximations character weighting in lower-level analysis 1a (same as Fig. 9), showing character changes (ACCTRAN optimization).

the analysis, and it is probably responsible for the rather different tree topology in the third analysis, as partially revealed by the elimination of *A. demialba*. Usage of several outgroup combinations may help to reveal such 'problem' taxa and provide greater confidence through widely supported tree topologies.

In all analyses, use of SACW greatly improved strict consensus tree resolution, but in the lower-level analysis always resulted in tree topologies not found in the original

set of equally weighted MPTs. A clear example is *A. pollina*, which appears in equally weighted analyses as sister to *capucinus* + *barnesia* + *diazi*, or as part of a polytomy, never within the *phylaca*-group, but after SACW moves to become the sister species of *thesprotia*, nested deep within the *phylaca*-group. Brower (2000) illustrates another good example of this effect with the apparent paraphyly of the almost certainly monophyletic nymphalid tribe Ithomiini after SACW.

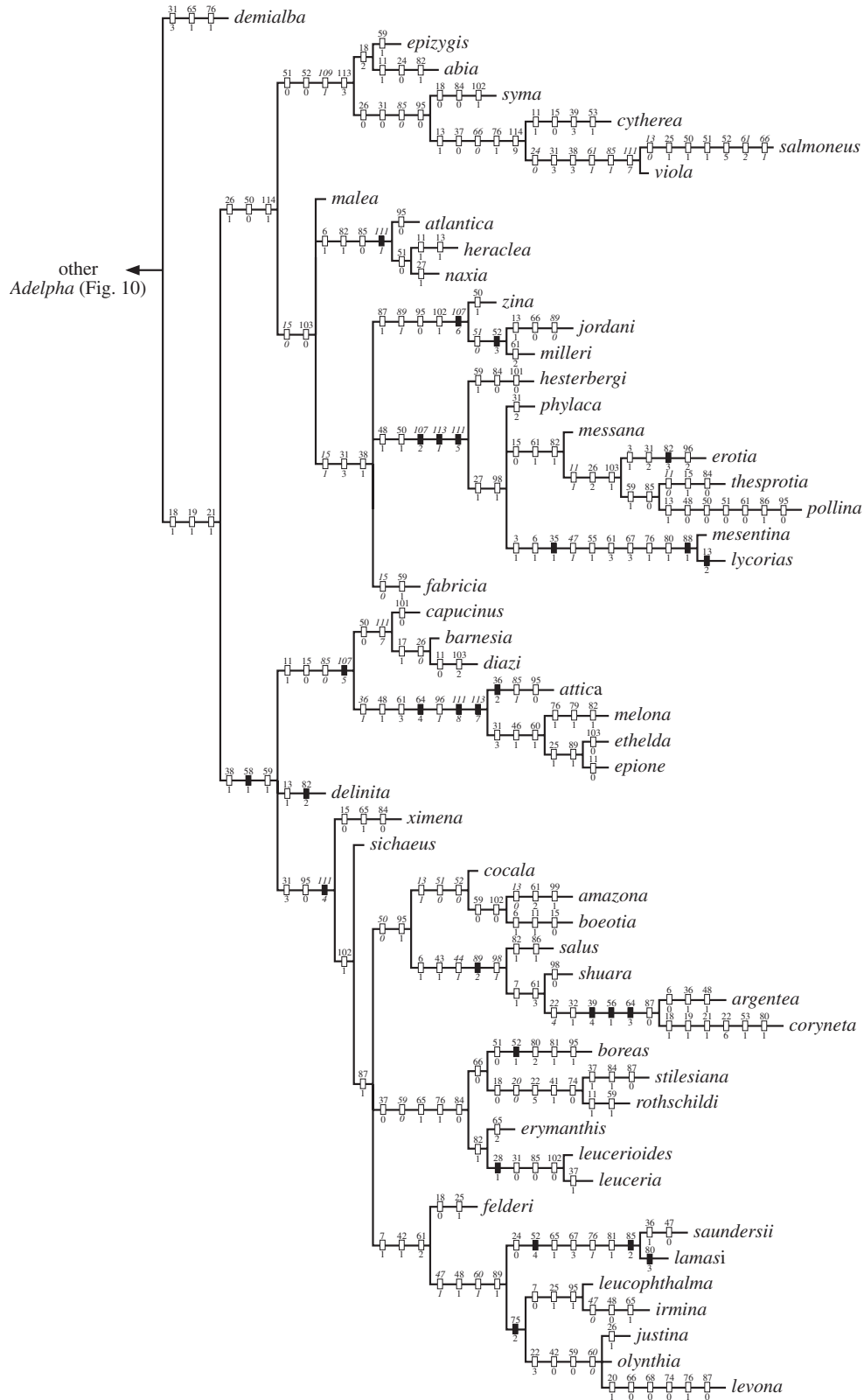


Fig. 11. Lower half of strict consensus of 13 124 most parsimonious trees after successive approximations character weighting in lower-level analysis 1a (same as Fig. 9), showing character changes (ACCTRAN optimization).



Fig. 12. Cladograms illustrating hypothesized relationships between *Adelpha* species resulting from analysis of adult characters only, with *Parasarpa zayla* and *Sumalia dudu* as outgroup species (lower-level analysis 1b). A, Strict consensus of 100 000 most parsimonious trees from equal weighted analysis; B, strict consensus of 115 most parsimonious trees resulting from successive approximations character weighting.

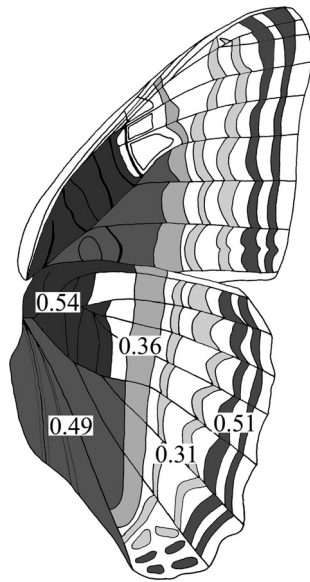


Fig. 13. Average consistency index of characters in different areas of the wing (forewing and hindwing pooled). Consistency indices were derived from the lower-level analysis, with *Parasarpa zayla* + *Sumalia dudu* as outgroup species, and from the higher-level analysis where characters were excluded from the former analysis. Shaded regions range from 20 to 80% grey, proportional to the average consistency index of characters in those regions. Unshaded regions provided no characters.

Changes in topology after SACW are due to one set of characters supporting a competing topology being down-weighted for their poor performance elsewhere in the tree. This may or may not be desirable, depending on how remote the clade is that most affects the consistency index of the characters in question. The best way to reduce this problem is to successively remove well supported basal clades from an initial tree, reweight characters to unity then perform SACW again on individual clades. I explored this approach in *Adelpha*, but the weak support of nodes at the base of the tree, after removal of the *alala*- and *serpa*-groups, prohibited any further progress being made.

Monophyly of *Adelpha*

The monophyly of *Adelpha* is strongly indicated in this study, supported by five synapomorphies, including: the orange inner postdiscal series in the dorsal forewing apex (23: 1, Fig. 2V), fusion of the postdiscal series on the dorsal forewing (24: 1, Fig. 2V), the presence of a dark line (basal streak) at the base of the ventral hindwing discal cell (62: 1, Figs 1, 3Y), a dark stripe along vein 3A on the ventral hindwing (68: 1; Figs 1, 3Gg) and a dark stripe in the middle of cell 3A–2A on the ventral hindwing (74: 1; Figs 1, 3Y, Z).

The suspicions of Aiello (1984) and Otero & Aiello (1996) that the genus might be para- or polyphyletic with respect to

certain Asian limenitidines were largely inspired by the distinctive immature stage morphology of several derived *serpa*-group members and their rather divergent male genitalia. In most *serpa*-group species, the valva lacks the clunacula, and the aedeagus has an internal spiny pad, both character states that only occur in species outside the *Limenitis* group of genera, like *Neptis*. However, the immature stage morphology of the primitive *serpa*-group species *A. bredowii* is much more typical of *Adelpha* (Harry, 1994), and the small clunacula in *A. zea* supports the interpretation that its absence in other *serpa*-group species represents a loss. Four of the five synapomorphies for *Adelpha* (all except 62: 1) are present in the *serpa*-group, arguing for its inclusion in *Adelpha*. Although current evidence suggests that the *serpa*-group is not the most basal within *Adelpha*, making consideration of separate generic recognition not worthwhile (the name *Heterochroa* Boisduval would be available), confirmation of its phylogenetic position would still be desirable.

Evaluation of clades and species groups within *Adelpha*

The first and second set of lower-level analyses sometimes produced conflicting results in comparison with the third analysis. Because the former two analyses produced consensus trees for *Adelpha* compatible in overall structure with all equally weighted analyses and the higher-level analysis, these results are regarded as the best current hypothesis of *Adelpha* relationships (Figs 9–11). In a revision of *Adelpha* (Willmott, 2003), I recognized a number of species groups (Fig. 8, Table 5) to aid taxonomic discussion. Some of these groups are supported as monophyletic, but others are not. The principal characters that support or refute the monophyly of major clades and species groups in the trees from all three sets of analyses are therefore discussed below.

The *alala*-group was recovered in all analyses and is convincingly diagnosed by several synapomorphies. It is placed as the basal clade in the genus in the majority of analyses, which is the best supported position based on current data. However, only a single character supports the monophyly of the remaining clade of *Adelpha* exclusive of the *alala*-group: the possession of dark lines where the legs fold against the thorax (4: 1, Fig. 2G). Because this character state also occurs in some outgroup taxa, and given the lightening in markings of the ventral wing surface of *alala*-group members, confirmation of this basal topology is desirable.

The *serpa*-group is the most strongly supported clade within the genus, with numerous synapomorphies. Among these, the restriction of red-brown scaling in the dorsal forewing discal cell to a dense patch anterior of the basal streak (16: 1, Fig. 2L), the absence of a basal streak in the ventral forewing cell (32: 1, Fig. 3B), the spiny pad in the aedeagus (90: 1, Fig. 4B) and the loss of clunacula in the male genitalia (99: 1, Fig. 4P) are particularly clear. Within the clade there is also substantial, well supported structure, with the North American species *A. bredowii* consistently

Table 5. Comparison between the species groups proposed for *Adelpha* based on immature stage characters by Aiello (1984, 1991) and Otero & Aiello (1996), and those proposed by Willmott (2003) and this study.

Species groups proposed by Aiello and Otero (several papers)	Species groups of Willmott (2003)	Status
Group I: <i>serpa, radiata?, paraena</i>	<i>serpa</i> -group: <i>bredowii, diocles, herbita, zea, nea, paroeca, paraena, radiata, serpa, seriphia, hyas</i>	Monophyletic
Group II: <i>phylaca, thesprotia, messana, mesentina, lycorias, abyala, sp.</i>	<i>phylaca</i> -group: <i>phylaca, thesprotia, messana, erotia, mesentina, lycorias</i>	Monophyletic (EW) or paraphyletic (SACW)
Group III: <i>heraclea, zina</i>	–	Polyphyletic
Group IV: <i>viola, salmoneus, cytherea</i>	–	Monophyletic (1a, 2, 3), polyphyletic (1b)
Group V: <i>iphichus/iphicleola</i>	<i>iphichus</i> -group: <i>calliphane, mythra, poltius, falcipennis, gavina, basiloides, plesaure, thoasa, thessalia, iphichus, iphicleola, abyala</i>	Paraphyletic (1a, 2), polyphyletic (1b: EW, 3b), monophyletic (1b: SACW)
Group VI: <i>basiloides, plesaure</i>	Included within <i>iphichus</i> -group	Monophyletic
Group VII: <i>cocala, leucophthalma</i>	<i>cocala</i> -group: <i>erymanthis, sichaeus, rothschildi, stilesiana, boreas, cocala, felderi, leucophthalma, irmina, saundersii, lamasi, salus, shuara, argentea, coryneta, jordani, zina, milleri, justina, olynthia, levona</i>	Monophyletic (higher-level analysis), polyphyletic (lower-level analyses)
Group VIII: <i>alala, aricia?, corcyra?, tracta?, pithys?, donysa?</i>	<i>alala</i> -group: <i>alala, aricia, corcyra, tracta, pithys, donysa</i>	Monophyletic

'1a', analysis number, if none given then same in all analyses; EW, with equally weighted characters only; SACW, with successive approximations character weighting only.

appearing as the most basal (Fig. 10). Although *A. gelania* was placed as the sister species to this clade, with the presence of iridescent blue scaling in the dorsal forewing cell (9: 1, Fig. 2L) as a synapomorphy, this is an intraspecifically variable character and both the bootstrap value and the decay index are low.

The other *Adelpha* typically form a clade with the following synapomorphies: a black lateral stripe on the labial palpi (1: 1, Fig. 2C), no long black hairs ventrally on labial palpi (2: 1, Fig. 2C) and an even forewing postdiscal band (20: 1, Fig. 2W) (Fig. 10). Of these, the first two characters are most convincing, but both also recur in parallel in a derived clade within the *serpa*-group. Nevertheless, the rescaled decay index from SACW analysis 1a is relatively high (3.9). The alternative topology of analysis 3, in which the *serpa*-group is nested deep within a paraphyletic assemblage of *iphichus*-group (and other) species, seems less likely, conflicting with all equally weighted analyses, requiring extra steps in the first two clear-cut characters and with no strong supporting synapomorphies.

Adelpha fessonia is typically sister to the other *Adelpha* (except in SACW analysis 3, with *Parasarpa zayla* and *Parasarpa zulema* as outgroup), which share brown rather than red sparse scaling in the dorsal forewing discal cell

(12: 1, Fig. 2R), loss of the third discal cell bar (37: 1, Fig. 3I) and a dark vein 3A on the ventral hindwing (69: 1, Fig. 3Gg). Both of these clades are also supported by modest rescaled decay indices (2.8, 1.9) in analysis 1a.

Basal to this latter clade of 'derived *Adelpha*' are the species that I refer to as the *iphichus*-group (Willmott, 2003). Although a paraphyletic assemblage in all analyses that include all characters, they occur as a monophyletic group in the SACW analysis of adult characters only (analysis 1b, Fig. 12B), diagnosed by characters 53: 1 (Fig. 3H) and 54: 1 (Fig. 3D), the distinctive shape of the forewing subapical marking. Because none of the internal nodes within the paraphyletic assemblage is strongly supported, or diagnosed by any immature stage characters, the relationships of these species remain unclear.

Remaining *Adelpha*, excluding the enigmatic species *A. demialba*, share the following synapomorphies: a fused postdiscal band and postdiscal series on the dorsal forewing (18: 1, 19: 1; Fig. 2Z) and an orange upper postdiscal band on the dorsal forewing (21: 1, Fig. 2Z). Despite a low decay index and bootstrap support, this nevertheless seems a likely clade. Within this clade occur a number of small clades of three to seven species, whose interrelationships are currently unclear, and a larger group of species that I call the *cocala*-group

(Willmott, 2003). The *phylaca*-group is supported by strong adult (27: 1, 98: 1; Figs 2Kk; 4N) and immature stage (107: 2, 113: 1; Fig. 5H) synapomorphies, but the placement of *A. pollina*, whose immature stages are unknown, and for which one adult character was coded as equivocal, is an unlikely member inserted into the clade only after SACW.

I treated five species as the '*capucinus*-group' (Willmott, 2003) based on a number of shared wing pattern and genitalic characters, and although three of these species form a clade in the current analyses, the other two, *A. fabricia* and *A. epizygis*, are far removed. *Adelpha epizygis* is placed as sister to *A. abia*, a highly unlikely position based on the large number of differing ventral surface pattern elements, and one that results principally from a shared dorsal pattern that is probably the result of mimicry (18: 2, Fig. 2N). Monophyly of the group, however, is perhaps also unlikely.

I referred to twenty-one species of *Adelpha* sharing a distinctive, rounded corpus bursae in the female genitalia (Willmott, 2003; not coded due to variation elsewhere in the genus), which also lacks paired bands of strongly sclerotized signa (102: 1, Fig. 4R), as the *cocala*-group (Willmott, 2003). The majority of these species cluster together in all analyses, but additional species not possessing these characters (*leuceria*, *leucerioides*, *boeotia*, *amazona*) are frequently inserted, and three species (*zina*, *milleri*, *jordani*) are usually omitted. *Adelpha leuceria* and *leucerioides* are plausible members based on a large number of shared characters with *A. erymanthis*, but the placements of the other anomalous species seem spurious and open to further study. In particular, immature stages and one ventral wing pattern character (Willmott, 2003) strongly support the species *cocala*, *felderi*, *leucophthalma* and *irmina* as a clade that was never recovered in any analysis. Mimicry is at its most rampant among the 'derived *Adelpha*', with its greatest potential to erase phylogenetic signal in wing pattern characters.

Comparison with previous studies

The results support the assertions of Moss (1933) and Aiello (1984) that dorsal wing pattern is often a poor guide to phylogenetic relationships in *Adelpha*. The three main dorsal wing patterns in the genus, each of which represents a sympatric mimicry ring (Willmott, 2003) and was used as a principal character to define species groups by earlier authors (Godman & Salvin, 1884; Fruhstorfer, 1915), are only weakly constrained by phylogeny. Figure 9 illustrates membership of these mimicry rings, named after prominent species members ('ipichlus', Fig. 2X; 'thesprotia', similar to Fig. 2Cc; 'salmonus', with an oblique orange forewing band). In most cases, similar dorsal wing patterns differ in finer detail, suggesting independent gain, or represent convergence through expression of non-homologous pattern elements (Willmott, 2003).

The species relationships proposed by Aiello (1984, 1991) and Otero & Aiello (1996), based on immature stages, and, in a few cases, male genitalic characters, are substantially

supported (Willmott, 2003; Table 5). Because the great majority of included character information is from the wing pattern, it is apparent that, with careful attention to homology, wing pattern may still provide significant phylogenetic signal, even when under strong selection for mimicry. The results here further indicate that a number of species included by Aiello and Otero within various groups do not appear to be related, and most groups include many more species than those initially included.

Of the groups proposed by Aiello and Otero, 'Groups II' (*phylaca*-group), 'IV' (*cytherea*-group) and 'VIII' (*alala*-group) are monophyletic groups that already include most or all members. 'Group I' is monophyletic but includes only three of the eleven species in the strongly supported *serpa*-group. 'Group VII' represents two closely related species (see above) that probably fall within a much larger clade, the *cocala*-group, although the cladistic analyses here do not support this hypothesis. 'Group III' is not monophyletic, 'Group V' contains only a single species and 'Group VI' contains the parapatric sister species *A. basiloides* and *A. plesaura*, which may be members of a larger clade, the *ipichlus*-group.

Recently, Freitas *et al.* (2001) described the immature stages of two southeast Brazilian species, *A. mythra* and *A. syma*. They regarded both as belonging to Aiello's 'Group VII' (see Table 5) based on 'scolus shape and the general pattern of the larvae, and the general form of the pupae', but the cladistic analyses here strongly refute this hypothesis. Instead, *A. syma* is sister to Aiello's 'Group IV', whereas *A. mythra* is placed in the paraphyletic *ipichlus*-group.

Evolution of the genus

Origin of Adelpha. The species of *Adelpha* are the only Limenitidini in the Neotropical Region, and with the four North American *Basilarchia* species, which themselves form a strong clade, represent the only New World representatives of this tribe. Brown & Heineman (1972) were the first to suggest that *Adelpha* and the North American *Basilarchia* might not be closely related, and probably resulted from separate invasions of the New World. The results here support this theory (Fig. 6C).

The North American species are apparently most closely related to several Palearctic taxa, including *Limenitis populi* and *Ladoga* Moore. *Limenitis populi* shares the same larval food-plant as the North American species, and has extremely similar immature stages, whereas adults of other species, such as the rare east Asian *Limenitis dubernardi* Oberthür, are even more similar in wing pattern. The North American species probably represent, as Brown & Heineman (1972) suggest, radiation from a relatively recent invasion by a single ancestral species across the Bering Strait from the eastern Palearctic.

The closest relatives to *Adelpha* also appear to lie in eastern Asia, with the majority being fairly uncommon montane species (Moore, 1898; Haribal, 1992). Like the

most basal species in *Adelpha*, larvae of *Sumalia dudu*, the sister to *Adelpha* in this study, also feed on Caprifoliaceae, as do *Ladoga* and some *Athyma* Westwood (Ackery, 1988; Igarashi & Fukuda, 1997, 2000). The ancestor of *Adelpha* probably therefore also fed on this plant family. In addition, larvae of several temperate region limenitidines such as *Ladoga* and *Limenitis* (e.g. Boudinot, 1986, 1987, 1988), and *Basilarchia* (e.g. Howe, 1975), are known to make leaf shelters for hibernation, a behaviour that has apparently been co-opted in primitive *Adelpha* for protection, but is not known elsewhere in the genus (Otero & Aiello, 1996; Willmott, 2003). The much greater diversity and geographical range of *Adelpha* suggests a colonization of the New World earlier than that of *Basilarchia*, although probably by the same route.

Major ecological shifts and diversification. The hypothesis that ancestral *Adelpha* fed on Caprifoliaceae is relevant to understanding the evolution of the genus. There is no evidence for this plant family in continental South America, the current centre of diversity for *Adelpha*, prior to the formation of the Panamanian isthmus a mere three million years ago (Gentry, 1982; Burnham & Graham, 1999). Although there are virtually no known time scales for butterfly diversification, because of the poor fossil record, a molecular clock for *Heliconius erato* divergence (Nymphalidae: Heliconiinae) (Brower, 1994) and a recently discovered fossil Riodinidae (Papilionoidea) (J. Hall, personal communication) suggest that butterfly species diverged millions of years before present, rather than tens or hundreds of thousands of years. It is therefore highly unlikely that *Adelpha* diversified within South America only after colonization by the most primitive species. Perhaps the most plausible explanation (Willmott, 2003) is an earlier invasion of continental South America by ancestral species whose larvae had already switched food-plants to a family then present in that region. A food-plant switch from Caprifoliaceae evidently occurred early in the evolution of the genus: *A. bredowii* feeds mostly on oak (*Quercus*, Fagaceae), whereas other primitive species, like *A. fessonia*, feed on Rubiaceae (references in Willmott, 2003). The *alala*-group and *A. bredowii* are confined to plants occurring in temperate environments, so a switch to Rubiaceae, which is highly diverse in tropical and temperate habitats (Gentry, 1993), may have been crucial in permitting the early diversification of the genus into the Neotropical lowlands. Indeed, 50% of species whose food-plants are known feed on Rubiaceae (Willmott, 2003), and this family is particularly prevalent in more derived *Adelpha*.

Although recent molecular phylogenies place Rubiaceae and Caprifoliaceae relatively far apart within the Asteridae (Savolainen *et al.*, 2000; Bremer *et al.*, 2001), support for branches between them is low and previously the two have been regarded as close relatives, even if not a monophyletic group (e.g. Cronquist, 1988). It seems likely that some shared plant chemistry makes food-plant switching between these two families relatively easy, as other tropical Asian Limenitidina (e.g. *Athyma*) as well as unrelated Lepidop-

tera, like *Hemaris* Dalman (Sphingidae), feed on both plant families. However, with little knowledge of the chemicals that mediate butterfly food-plant choice, and only fragmentary data on plant secondary chemicals for these families (e.g. Gibbs, 1974), it is not clear what this shared chemistry might be.

There is comparatively little evidence from range positions of closely related species for allopatric geographical speciation in *Adelpha* (Willmott, 2003), with the majority of closely related species occurring sympatrically. Either the majority of speciation in *Adelpha* occurred sufficiently long ago to allow ranges to now overlap, or speciation may have been frequently macro-sympatric. In *Adelpha*, a plausible mechanism for speciation is through shifts in mimetic ring colour patterns (Bates, 1862; Joron & Mallet, 1998; Mallet & Joron, 1999). Virtually all *Adelpha* are strongly mimetic, usually of other *Adelpha* (Willmott, 2003). Mimetic ring colour pattern shifts, which often occur within single populations or between parapatric geographical races in *Adelpha*, could lead to new species through disruptive selection, as non-mimetic hybrids between different mimetic ring phenotypes are strongly selected against (Joron & Mallet, 1998; Mallet & Joron, 1999). The SACW cladogram (Fig. 9) shows that among species in the more derived, lower half of the genus mimetic pattern switches frequently, as expected if mimicry shifts accompany speciation.

Classification of Limenitidini

Although it was not my initial goal to examine the classification of Limenitidini, I assessed much of the currently available information to choose appropriate outgroups for the analysis of *Adelpha*. The existing supra-specific classification within Limenitidini proved to be chaotic, especially within Limenitidina (*sensu* Harvey, 1991), with little consensus as to generic or subtribal limits. In addition, recent excellent studies of immature stages (Amiet, 1997, 1998a,b, 1999, 2000a,b, 2002; Igarashi & Fukuda, 1997, 2000) reveal several obviously misplaced taxa. I therefore briefly review the subtribal classification, which will hopefully help guide future phylogenetic analysis.

The majority of modern authors recognize three or four subtribal divisions within Limenitidini, corresponding to groups of various taxonomic rank recognized by earlier authors (see review in Chermock, 1950, Hemming, 1960, Eliot, 1978 and Harvey, 1991), including Parthenina, Euthaliina, Limenitidina, and sometimes Neptina. However, Hemming (1960) described an additional four supra-generic names in an obscure publication that seems to have been overlooked by most subsequent authors. These include 'Bebeariini' (type genus *Bebearia* Hemming, with a number of other African genera), 'Neurosigmatini' (type and only genus *Neurosigma* Butler), 'Abrotini' (type and only genus *Abrota* Moore) and 'Chalingini' (type and only genus *Chalinga* Moore). The name Chalingini was subsequently described again, as a junior homonym, by Chou (1998), who also included three additional distinctive genera: *Auzakia* Moore,

Seokia Sibatani, and *Bhagadatta* Moore. The subtribal positions of all of these genera are discussed below.

The majority of these subtribal divisions were based largely on wing venation, a highly variable character source (it is even in a single species of *Adelpha*, *A. lycorias*), and there is no evidence whether putative diagnostic characters (e.g. Hemming, 1960; Eliot, 1978) represent synapomorphies or symplesiomorphies. Chermock (1950) recognized no formal subtribal groupings, but nevertheless made the most extensive survey of adult and immature stage morphology in the tribe to date, and his (admittedly not explicitly derived) phylogenetic tree corresponds reasonably with current knowledge. Figure 14 summarizes relationships between genera and subtribes of Limenitidini, as largely proposed by Chermock (1950), with several changes to reflect new knowledge (Amiet, 1997, 2000a,b; Igarashi & Fukuda, 1997, 2000).

The type genus of Chalingina, *Chalinga*, and an additional monotypic genus included in that subtribe by Chou (1998), *Seokia*, probably do not belong in Limenitidini, and are omitted from this classification. *Chalinga* was established for *Limenitis elwesi* Oberthür, an enigmatic species whose immature stages and taxonomic relationships are unknown. Chermock (1950) excluded it from Limenitidini on the basis of wing venation and male genitalia; most importantly this species lacks the spur on the forewing representing vein 1A that characterizes the majority of the tribe (Chermock, 1950). The morphology of *Seokia pratti* (Leech) is similar in all these respects to *Chalinga*, also supporting its exclusion from the tribe.

There is no strong evidence for a close relationship between *Lebadea* C. Felder and *Parthenos* Hübner, making Parthenina (*sensu* Eliot, 1978; Harvey, 1991) polyphyletic.

The immature stages of *Lebadea martha* are not remotely similar to *Parthenos*, but instead are typical of Limenitidina (Igarashi & Fukuda, 2000: plate 181; see below). The male genitalia of *Lebadea* also show similarities to *Neptis*, with the relatively small uncus and tegumen and slender uncus. Chermock (1950) also placed *Lebadea* next to *Limenitis*, far from *Parthenos*. I therefore remove *Lebadea* to the Limenitidina.

Chermock (1950) placed the Sino-Himalayan *Bhagadatta austenia* in *Limenitis*, but it must be assumed that he examined no specimens of this rare species. The genitalia are quite unlike those of any *Limenitis* group species and the hindwing discocellular vein is present, as in *Parthenos* and *Cymothoe* Hübner but not in any genera related to *Limenitis*. The distinctive male genitalia of *Bhagadatta austenia* were also noted by Chou (1998), who placed it in Chalingina, and Morishita (1995), who suggested that the species did not even belong in Limenitidini, but instead was closely related to *Pseudergolis* C. & R. Felder in Pseudergolini Jordan 1898. Morishita (1995) also suggested that knowledge of the immature stages of *Bhagadatta austenia* would confirm this placement. The subsequent figure of the fifth-instar larva and pupa in Igarashi & Fukuda (2000: plate 185) indicates that there is, however, no close relationship between *Bhagadatta austenia* and Pseudergolini. Instead, the coloration and scoli arrangement of the fifth-instar larva are similar to *Parthenos sylvia*, as is the shape of the juxta in the male genitalia (91: 3), and the forewing venation, with vein 1A preserved as a short spur, is typical of Limenitidini. Unfortunately, the head capsule of the fifth-instar larva is not clearly visible in Igarashi & Fukuda (2000), and it is unclear whether it is covered with short chalazae, as in *Parthenos* and Limenitidina, or is smooth, as

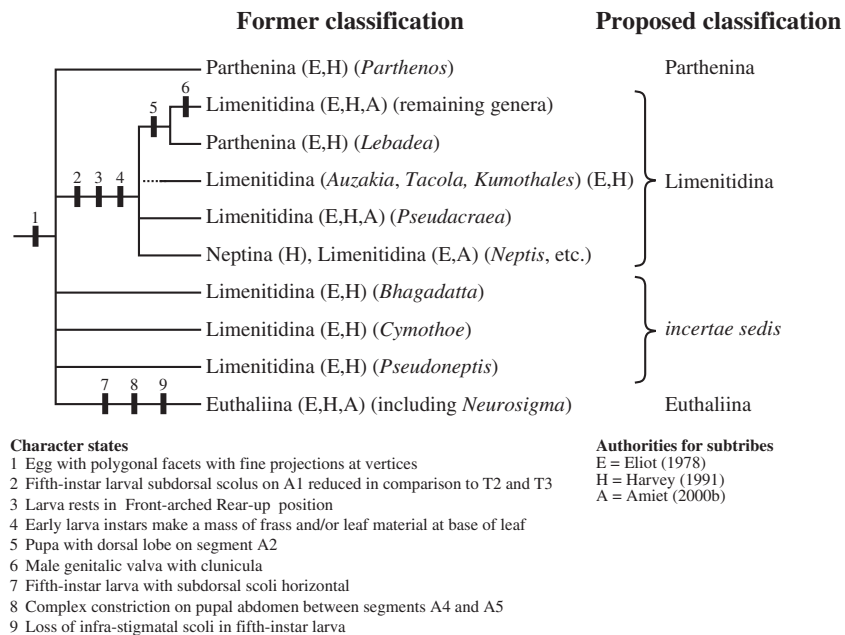


Fig. 14. Classification and hypothesis of relationships between genera and groups of Limenitidini.

in *Cymothoe* and the Euthaliina (Amiet, 2000a). The pupa is similar in shape to both *Parthenos* and *Cymothoe*, and remarkably similar in colour pattern to *Cymothoe* (Amiet, 2000a). As noted by Amiet (2000a), *Bhagadatta* clearly does not belong in the Limenitidina, and it is for the present treated as *incertae sedis*, along with *Cymothoe*.

The African *Cymothoe*, including *Harma* Doubleday (see Amiet, 2000a), differs from Euthaliina in having vertical larval subdorsal scoli, but resembles that subtribe in the head capsule lacking chalazae (e.g. Amiet, 1997, 2000a). It was included by Hemming (1960) in Bebeariina, and by Harvey (1991) in Limenitidina, although Chermock (1950) regarded it as a primitive member of the tribe. Chermock's insight is supported by immature stage morphology, which lacks the synapomorphies that characterize Limenitidina and Euthaliina (Amiet, 2000b) (Table 6). Amiet (2000b) suggested that *Cymothoe* might merit its own subtribe, although a relationship with Euthaliina seems plausible based on the similarities of the first-instar larva (Amiet, 2000b) and smooth larval head capsule, among other characters (Table 6). However, until a thorough phylogenetic analysis of the tribe is completed, its subtribal status should be treated as *incertae sedis*.

Two additional, monotypic, genera included in Limenitidina by Harvey (1991), *Pseudoneptis* Snellen and *Kumothales* Overlaet, are also of uncertain phylogenetic position. The immature stages of *Pseudoneptis* lack the synapomorphies of Limenitidina (Table 6) and more resemble those of *Cymothoe*, with a suite of autapomorphies (Amiet, 2002). The subtribal placement of the genus is therefore regarded as *incertae sedis*. The life history of *Kumothales* is unknown and so for the present it is best left in Limenitidina.

Euthaliina, as formerly recognized by most previous authors, is well supported as a monophyletic group by the highly distinctive horizontal arrangement of the subdorsal scoli in the larva, correlated with the loss of the infra-stigmatal scoli. Amiet (2000a) also cites as additional synapomorphies a complex constriction of the pupal abdomen between segments A4 and A5, and secretion of a viscous, repellent substance by the prepupa, although the latter remains to be confirmed in non-African euthaliine genera.

The type genera of Bebeariina Hemming (*Bebearia*) and Abrotina Hemming (*Abrota*) have a typically euthaliine larval subdorsal scoli arrangement, in addition to a pupal shape characteristic of a number of euthaliine genera, including *Euthalia* (Amiet, 1998a; Igarashi & Fukuda, 2000). Both are therefore regarded as subjective junior synonyms of Euthaliina.

Neurosigma, the type genus of Neurosigmatina Hemming, was treated as a synonym of *Euthalia* by Chermock (1950), and without additional information it is more conservative to retain it in Euthaliina (e.g. Harvey, 1991).

Neptina, long considered a separate group from Limenitidina, seems to be a well-supported monophyletic group (see Chermock, 1950). However, although Harvey (1991) and Chou (1998) retained these two groups as distinct taxa, Chermock (1950), Eliot (1978) and Amiet (2000b) regarded

Neptina as a specialized clade within Limenitidina, and as such not worthy of preservation. Chermock (1950) and Amiet (2000b) proposed several morphological and ethological characters as synapomorphies of this expanded group of genera, which constitutes a revised Limenitidina equivalent to the '*Limenitis* line' of Chermock (1950) (Table 6).

Chermock (1950) treated the distinctive genus *Auzakia* Moore (included in *Chalingina* by Chou, 1998) as a synonym of *Euthalia* Hübner (Euthaliina), without comment, but the shape of the aedeagus and its internal spiny pad is almost identical to that of most Limenitidina, where it was placed by Harvey (1991). Like *Auzakia*, the type species of *Tacola* Moore, *Tacola larymna* (Doubleday), also lacks a clunicula, and the aedeagus is distinct from all other *Limenitis* group species, but *Tacola* was nevertheless treated by Chermock (1950) as a synonym of *Limenitis*. Both genera are plausible basal members of Limenitidina, but knowledge of the immature stages would help to confirm their subtribal position.

Within Limenitidina, a further group of genera, including *Lebadea* and Chermock's (1950) '*Limenitis*', are defined by possession of an anteriorly projecting dorsal lobe from segment A2 of the pupa. Although Chermock (1950) considered this lobe to be present in *Neptis*, it is not apparent in any of the species that I have seen (Igarashi & Fukuda, 1997, 2000; Amiet, 2000b). Chermock may have been referring to a dorsal 'hump' which does occur in *Neptis*, but in *Lebadea* and the *Limenitis* group of genera the lobe always projects anteriorly, and I consider it a distinct character state. Chermock's (1950) genus '*Limenitis*' includes a group of genera diagnosed by a spinose lobe projecting dorsally from the inner base of the valva (termed the 'clunicula' by Fruhstorfer, 1915), secondarily lost in the *Adelpha serpa*-group.

In summary, until more evidence is available from a comprehensive morphological and molecular phylogenetic analysis, I believe that three subtribes should be recognized: Parthenina, including *Parthenos* only; Euthaliina, as conceived by most previous authors; and Limenitidina, containing the remaining genera (Fig. 14), with the exception of *Cymothoe*, *Pseudoneptis* and *Bhagadatta*, which are regarded as *incertae sedis*. The monotypic genera *Seokia* and *Chalinga* probably do not belong in Limenitidini, at least as currently conceived, and the subtribal positions of *Neurosigma* (Euthaliina), *Auzakia*, *Tacola* and *Kumothales* (Limenitidina) require confirmation. Characters that provide, or have been suggested to provide, phylogenetic information at the subtribal level within Limenitidini, and within Limenitidina, are summarized and evaluated in Table 6. Many other characters providing information within Euthaliina and at lower levels are discussed by Amiet (1998a,b, 1999). Characters are listed in putative phylogenetic order, and subtribal names are as proposed in this paper. A number of character states may prove to be synapomorphies but are difficult to evaluate without a better knowledge of the sister group of Limenitidini.

The monophyly of virtually all currently recognized limenitidine genera, especially in Limenitidina, is untested

Table 6. Characters of Limenitidini.

Character	Source	Distribution
Synapomorphies		
Subdorsal scoli of fifth-instar larva significantly reduced on A1 in comparison with T2 and T3	Chermock (1950)	Synapomorphy for Limenitidina. Slight reduction of scoli on T2 and T3 also occurs in some <i>incertae sedis</i> species (<i>Parthenos</i> and some <i>Cymothoe</i>), but not so noticeably as in Limenitidina.
'Front-arched rear-up' defensive posture (Aiello, 1984: 14)	Amiet (2000b)	Synapomorphy for Limenitidina, although not reported or known for a number of constituent genera.
Construction of a mass of leaf material or frass, or both, at the base of the feeding 'perch', or hanging beneath	Amiet (2000b)	Synapomorphy for Limenitidina. Reported in <i>Adelpha</i> (Aiello, 1984), <i>Neptis</i> , <i>Pseudacraea</i> (Amiet, 2000b), <i>Limenitis populi</i> (Boudinot, 1987), <i>Ladoga camilla</i> (Boudinot, 1988), <i>Ladoga reducta</i> (Boudinot, 1986), <i>Moduza procris</i> (Morrell, 1954).
Anteriorly projecting dorsal lobe on segment A2 of pupa	Chermock (1950)	Synapomorphy for <i>Limenitis</i> group of genera + <i>Lebadea</i> . Not checked in <i>Tacola</i> or <i>Auzakia</i> , which lack a clunicula in the male genitalia.
Spinose lobe projecting dorsally from the inner base of the male genitalic valva (clunicula)	Chermock (1950)	Synapomorphy for <i>Limenitis</i> group of genera, although secondarily lost in one group of <i>Adelpha</i> .
Fifth-instar larval subdorsal scoli held horizontally, pressed to leaf	Chermock (1950)	Synapomorphy for Euthaliina.
Loss of infra-stigmatal scoli in fifth-instar larva	Amiet (2000a)	Synapomorphy for Euthaliina.
Complex constriction of pupal abdomen between segments A4 and A5	Amiet (2000a)	Synapomorphy for Euthaliina.
Uncertain		
No construction of leaf 'perch' in early instar larva	Amiet (2000a, 2002)	Synapomorphy for Euthaliina + <i>Cymothoe</i> + <i>Pseudoneptis</i> ? Many nonlimenitidines, and Limenitidina, extend leaf veins with frass to make a 'perch' on which they rest; the absence of this behaviour in Euthaliina and <i>Cymothoe</i> is a possible synapomorphy.
First-instar larva with smooth, glossy head capsule	Amiet (2000a, 2002)	Synapomorphy for Euthaliina + <i>Cymothoe</i> + <i>Pseudoneptis</i> ? According to Amiet (2000a, 2002), first-instar Limenitidina have a granulated, matt head capsule. The outgroup state is unknown.
Loss of chalazae on larval head capsule	–	Synapomorphy for Euthaliina + <i>Cymothoe</i> + <i>Pseudoneptis</i> ? Given the widespread distribution of chalazae among Nymphalidae, their absence in <i>Cymothoe</i> , <i>Pseudoneptis</i> and Euthaliina seems a possible synapomorphy.
Fifth-instar larva integument smooth, lacking secondary transverse folds	Amiet (2000a)	Synapomorphy for Euthaliina + <i>Cymothoe</i> + <i>Pseudoneptis</i> ? According to Amiet (2000a), the integument of fifth-instar Limenitidina is markedly folded and granulated, although this may not be visible in dead specimens due to inflation of the body. The outgroup state is unknown.
'Stereophory' (decoration of body with faecal pellets in first-instar larva)	Amiet (2000b)	Putative synapomorphy for Limenitidina (Amiet, 2000b), but also occurs in <i>Mahaldia</i> (Euthaliina) (Igarashi & Fukuda, 1997: plates 199, 200). Not reported in <i>Moduza procris</i> (Morrell, 1954) or <i>Adelpha</i> (Aiello, 1984) (both Limenitidina), or outside Limenitidini.
Base of pupal cephalic projections with round cross-section	Amiet (2000a)	Synapomorphy for Euthaliina + <i>Cymothoe</i> + <i>Pseudoneptis</i> ? Pupal cephalic projections are approximately triangular in cross-section in Limenitidina and <i>Parthenos</i> .
Short, spatulate primary setae on first-instar larva, presumed to assist in fastening faecal pellets	Amiet (2000b)	Only reported within Limenitidina (Amiet, 2000b), but not checked in Asian euthaliines like <i>Mahaldia</i> , which also exhibits stereophory. Euthaliina + <i>Cymothoe</i> possess thin, hairlike or ramified, tapering primary setae (Amiet, 1998a,b, 1999, 2000a).

Table 6. Continued.

Character	Source	Distribution
Secretion of a yellowish 'pre-nymphal substance'	Amiet (2000a)	Synapomorphy for Euthaliina? Prepupae of African Euthaliina are reported to secrete a viscous, possibly repellent substance just before pupation (Amiet, 1998a, 2000a).
Probable symplesiomorphies		
Several other defensive/resting postures (Aiello, 1984: 14)	Amiet (2000b)	Except for 'front-arched rear-up', other limenitidine groups show similar postures (see Igarashi & Fukuda, 1997, 2000).
Chalazae on head capsule in later instars	Amiet (2000b)	Occurs in other nymphalid groups, including Apaturinae, Satyrinae, Charaxinae (personal observation).
Striped, two-tone head capsule in later instars	Amiet (2000b)	Occurs in other nymphalid groups, including Apaturinae, Satyrinae, Charaxinae (personal observation).
Round 'pits' on surface of head capsule	Amiet (2000b)	Occurs in other nymphalid groups, including Apaturinae, Satyrinae, Charaxinae (personal observation).

(although much information is presented for African genera by Amiet (1997, 1998a,b, 1999, 2000a,b, 2002)), and such genera are typically based on a single or only a few characters. Authors, including myself, are forced to choose which generic name to use based largely on 'Gestalt'. Although the analysis here does not provide any test of the status of limenitidine genera (except *Adelpha*), there are several points of note. Following Chermock's (1950) lumping of all *Limenitis* group genera into a single genus, *Limenitis*, other authors have been gradually removing more phenotypically distinct species, leaving a phylogenetically meaningless residue. The SACW results suggest that '*Limenitis*', in the broad sense of some authors (i.e. including such species as *Ladoga reducta* and *Ladoga camilla*, and even the North American *Basilarchia*), may well be paraphyletic. It is suggested that the current trend towards recognizing more, smaller, phenotypically homogeneous genera (where names already exist) is the wisest course of action, until a thorough phylogenetic revision produces a stable generic classification.

Conclusions and future work

The results presented here, although beginning to reveal an overall phylogenetic framework for *Adelpha* that is relatively robust, as well as suggesting a number of well supported species relationships, are still very far from satisfactory. However, the results do point towards the species that must be included in any future analysis with additional character data.

Although wing pattern proved to be a most valuable source of characters, its phylogenetic utility in *Adelpha*, and no doubt in many other limenitidines, is limited by its high phenotypic plasticity. Within all Limenitidina examined, the extreme homogeneity in adult morphology left the majority of deeper nodes unresolved or poorly supported. The immature stages proved to be highly variable, perhaps surprisingly so, but also failed to indicate relationships in these areas of the phylogeny. Although immature stages are valuable at the subtribal level in Limenitidini and within the

Euthaliina, it is not clear whether they will ever provide sufficient data to be of use in inferring relationships among Limenitidina. Similarly, although immature stages have been seen as the key to understanding *Adelpha* phylogeny (Aiello, 1984, 1991; Otero & Aiello, 1996), it is highly unlikely that data will be available for enough species to fully realize the potential of this character source. Instead, molecular sequence data must surely be seen as the most promising future line of investigation into *Adelpha*, and limenitidine, evolution.

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Appendix 1

Characters used in the cladistic analysis. Codes: B = used in both the higher- and lower-level analyses; H = used only in the higher-level analysis; L = used only in the lower-level analysis. CI_{EW} = maximum consistency index in the equally weighted analysis; CI_{SACW} = maximum consistency index in the SACW analysis. Values are from lower-level analysis 1a, where available, otherwise from the higher-level analysis. Averages for character partitions are given in parentheses after the partition name.

Body ($CI_{EW}=0.62$; $CI_{SACW}=0.62$)

1(B). *Labial palpi laterally*: (0) white (Fig. 2B); (1) with a longitudinal black stripe (Fig. 2C); (2) with a longitudinal stripe of mixed brown and white scales (Fig. 2A) ($CI_{EW}=0.67$; $CI_{SACW}=0.67$).

In *Adelpha*, state 1 is clearly distinct from state 0. State 1 is a synapomorphy for the ‘derived *Adelpha*’ clade, as well as a clade of more derived *serpa*-group members. Some outgroup taxa have a mixture of darker scales forming a faint latitudinal line, which was coded as a distinct character.

2(B). *Labial palpi with dense long black hairs on ventral surface*: (0) present (Fig. 2A); (1) absent or short hairs (Fig. 2C) ($CI_{EW}=0.33$; $CI_{SACW}=0.33$).

Within *Adelpha*, this character correlates completely with 1, but not among the outgroup taxa.

3(B). *Dorsally behind eyes with white scaling*: (0) absent (Fig. 2D); (1) present (Fig. 2E) ($CI_{EW}=0.33$; $CI_{SACW}=0.33$).

State 1 is a synapomorphy for the *serpa*-group, also occurring in two other *Adelpha* species and several outgroup taxa.

4(B). *Ventral half of thorax where legs fold*: (0) pale (Fig. 2F); (1) dark (Fig. 2G) ($CI_{EW}=1$; $CI_{SACW}=1$).

State 1 is a synapomorphy for all *Adelpha* except the *alala*-group. Because the thoracic scales are frequently rubbed off through the handling of specimens during capture and preparation, insufficient specimens were available to code this character for three rare *Adelpha* species.

5(H). *Dorsal surface of abdomen*: (0) entirely dark (Fig. 2H); (1) with white band across base (Fig. 2I); (2) with brown band across base (Fig. 2J); (3) with lateral white spots (Fig. 2K) ($CI_{EW}=0.75$; $CI_{SACW}=0.75$).

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Venation ($CI_{EW}=0.17$; $CI_{SACW}=0.17$)

6(L). *Forewing discocellular vein*: (0) present (Fig. 4A); (1) reduced or absent ($CI_{EW}=0.17$; $CI_{SACW}=0.17$).

Forewing dorsal surface ($CI_{EW}=0.36$; $CI_{SACW}=0.34$)

7(L). *DFW discal cell with basal streak*: (0) visible (Fig. 2L); (1) not visible (Fig. 2Bb) ($CI_{EW}=0.17$; $CI_{SACW}=0.17$).

8(B). *DFW discal cell with basal streak*: (0) relatively far from costa, near middle of cell (Fig. 2Z); (1) near costal margin (Fig. 2L) ($CI_{EW}=0.5$; $CI_{SACW}=0.33$).

State 1 is a synapomorphy for the *serpa*-group.

9(B). *DFW discal cell with iridescent blue-green scaling*: (0) absent (Fig. 2M); (1) present (Fig. 2L) ($CI_{EW}=0.25$; $CI_{SACW}=0.2$).

Distinctive iridescent blue-green scaling in the DFW discal cell occurs in several outgroup taxa, but in *Adelpha* only in some *serpa*-group members and *A. gelania*, suggesting *A. gelania*, or *A. gelania* + *A. fessonia*, may be near to the base of the *serpa*-group.

10(B). *DFW discal cell with iridescent blue-green scaling*: (0) extensive, occurring basal of the first cell bar, between cell bars 2 and 3, and 3 and 4, filling most of the area basal of the first cell bar (usually) (Fig. 2L); (1) not extensive, confined to the anterior half of the space basal to the first cell bar, and (usually the anterior half of) the space between cell bars 2 and 3, not occurring between 3 and 4 (Fig. 2P) ($CI_{EW}=1$; $CI_{SACW}=1$).

11(B). *DFW discal cell with sparse paler scaling between cell bars 1 and 2, and 4 and postcellular*: (0) absent; (1) present (Fig. 2Q) ($CI_{EW}=0.08$; $CI_{SACW}=0.07$).

12(B). *DFW discal cell with sparse paler scaling between cell bars 1 and 2, and 4 and postcellular*: (0) red (Fig. 2Q); (1) brown (Fig. 2R) ($CI_{EW}=1$; $CI_{SACW}=1$).

State 0 occurs in the *serpa*-group, *A. fessonia* and *A. gelania*, whereas state 1 occurs only in more derived *Adelpha*.

13(L). *DFW anterior half of discal cell between cell bars 2 and 4*: (0) dark black-brown; (1) with sparse orange scaling (Fig. 2S); (2) with white scaling (Fig. 2T) ($CI_{EW}=0.2$; $CI_{SACW}=0.17$).

- 14(H). *DFW discal cell with white streak basal of first cell bar*: (0) absent; (1) present (Fig. 2Ee) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- 15(B). *DFW basal area with red-brown scaling*: (0) present (Fig. 2L); (1) absent ($CI_{EW} = 0.1$; $CI_{SACW} = 0.07$).
- 16(B). *DFW basal area with red-brown scaling*: (0) extending along the anal margin, in the basal area of the discal cell, and in cell 2A-Cu2 (Fig. 2R); (1) restricted to a dense patch anterior of the basal streak (Fig. 2L); (2) coalesced into bands (Fig. 2Dd) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

State 1 is a synapomorphy for the *serpa*-group.

- 17(L). *DFW cell Cu1-M3 with postdiscal band*: (0) present (Fig. 2L); (1) absent (Fig. 2Aa) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

This character is continuously variable in *A. paraena* and *A. radiata*, and was coded as equivocal. In *A. malea* it is racially dimorphic. In *Parthenos sylvia*, it is unclear whether the large white block in this cell, which forms part of the forewing band, represents this pattern element or the postdiscal series, and it was coded as equivocal.

- 18(B). *DFW cell Cu1-M3 with postdiscal band and postdiscal series*: (0) separate (Fig. 2U); (1) fused (Fig. 2Z); (2) touching (Fig. 2N) ($CI_{EW} = 0.1$; $CI_{SACW} = 0.1$).

In most species, these two elements are clearly separate or overlap entirely, except in three species in which they lie adjacent, which were coded as a distinct state. Fusion is inferred either from the ventral surface, if both band and series are still visible, or from a narrowing of forewing postdiscal marking towards the anal margin, and tracing of the position of where the distal edge of the postdiscal band is expected to lie from the anal margin on the DHW. In *A. rothschildi*, the postdiscal marking is narrow and oblique, and there is no indication as to whether it represents just the postdiscal band, series, or both, so it was coded as equivocal. The forewing inner postdiscal series is absent in a number of outgroup taxa and the character was therefore coded as equivocal.

- 19(B). *DFW cell M3-M2 with postdiscal band and postdiscal series*: (0) separate (Fig. 2M); (1) fused (Fig. 2Z) ($CI_{EW} = 0.41$; $CI_{SACW} = 0.39$).

In a large number of taxa, the postdiscal band is not visible on the DFW in cell M3-M2. However, when both postdiscal band and series were visible and clearly distinct on the VFW, and the postdiscal series on the DFW confined to the area of the postdiscal series on the VFW, they were coded as separate. In other cases, without such evidence, the character was coded as equivocal.

- 20(B). *DFW lower postdiscal band formed of*: (0) isolated spots, with black cutting in at the basal edge at veins, especially Cu2 (Fig. 2L); (1) contiguous spots forming a band with smooth distal and basal edges (Fig. 2W); (2) contiguous spots forming a band with uneven distal and basal edges (Fig. 2Ff) ($CI_{EW} = 0.22$; $CI_{SACW} = 0.2$).

- 21(L). *DFW upper postdiscal band*: (0) white, greyish-white or pale shading (Fig. 2L); (1) orange (Fig. 2Z) ($CI_{EW} = 0.14$; $CI_{SACW} = 0.14$).

State 0 represents a continuous variation.

- 22(L). *DFW upper postdiscal band*: (0) present equally in cells M3-M2 to M1-R5 and costa, filling each cell (Fig. 2Z); (1) present in cells M3-M2 to M1-R5 but reduced with diffuse scaling throughout (Fig. 2V); (2) present in cells M3-M2 to M1-R5 as isolated, elongate streaks (Fig. 2O); (3) present in cells M3-M2 to M1-R5 as small, isolated spots of variable size (Fig. 2Cc); (4) always present and filling cell M3-M2, variable in cells M2-M1 and M1-R5 (Fig. 2W); (5) present only in cells M2-M1 and M1-R5 (may extend slightly into M3-M2) (Fig. 2U); (6) present at posterior edge of M3-M2 only (Fig. 2M); (7) absent in all cells (Fig. 2X) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.17$).

The upper postdiscal band shows parallel variation in each cell in a number of species (e.g. band width in *A. alala* and relatives, presence/absence in *A. olynthia*) and in the majority of species it is either entirely present or absent. It was therefore coded as a single character, rather than split into distinct characters for each cell.

- 23(H). *DFW cells M2-M1 and M1-R5 with inner postdiscal series*: (0) white or paler ground colour (Fig. 2Gg); (1) orange (Fig. 2V) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.2$).

State 1 is a synapomorphy for *Adelpha*. It has been secondarily lost in a few *Adelpha* species, and independently gained in some outgroup taxa.

- 24(B). *DFW cell M2-M1 with subapical markings representing inner and outer postdiscal series*: (0) separate (Fig. 2Gg); (1) fused (Fig. 2V) ($CI_{EW} = 0.25$; $CI_{SACW} = 0.25$).

State 1 is a synapomorphy for *Adelpha*. It has been secondarily lost in four *Adelpha* species, and independently gained in *Basilarchia archippus*, a species that has undergone extreme fusion of pattern elements through mimicry with Danainae species.

- 25(L). *DFW with subapical spots (postdiscal series) anterior to vein M2*: (0) at least partially present (Fig. 2Z); (1) absent (Fig. 2Bb) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.17$).

- 26(B). *DFW subapical spot (postdiscal series)*: (0) larger in cell M2-M1 than in cell M1-R5 (Fig. 2Aa); (1) larger in cell M1-R5 than in cell M2-M1 (Fig. 2Y); (2) of similar size (Fig. 2F) ($CI_{EW} = 0.22$; $CI_{SACW} = 0.25$).

Ingroup taxa which have state 54: 1 were coded as equivocal for this character, as the narrowing of the subapical marking (i.e. the fused postdiscal series) towards the costa may also result from the loss of the outer postdiscal series in cell M1-R5. Among outgroup taxa, the postdiscal series are fused only in *Basilarchia archippus*, so remaining outgroup taxa were coded as equivocal for this character.

Hindwing dorsal surface ($CI_{EW} = 0.57$; $CI_{SACW} = 0.59$)

- 27(B). *DHW base of veins M2, M1 and Rs with scales*: (0) of similar colour and orientation to adjacent wing (Fig. 2Ll); (1) pale and densely bunched, randomly orientated (Fig. 2Kk) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.5$).

State 1 is a synapomorphy for the *phylaca*-group, but also occurs in *A. naxia* and *A. pollina*.

28(L). *DHW postdiscal band*: (0) white, at least along basal edge (Fig. 2Kk); (1) entirely orange (Fig. 2Ll) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

A number of *Adelpha* species variably approach state 1 in the Apure region of Venezuela. However, in all of these species the postdiscal band itself is not orange, but variably tinged orange from the coloration of the DHW postdiscal series. In only two species, *A. leuceria* and *A. leucerioides*, is the postdiscal band itself orange.

29(H). *DHW inner submarginal series*: (0) not visible or only as paler ground colour (Fig. 2Ii); (1) a white band of large spots (Fig. 2Oo); (2) a green band (Fig. 2Pp); (3) small white dots (Fig. 2Qq); (4) yellowish-brown crescents (Fig. 2Nn) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

30(H). *DHW with outer postdiscal series*: (0) even throughout (Fig. 2Ll); (1) reduced to form an isolated spot at tornus (Fig. 2Ii) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.25$).

State 1 appears to be a symplesiomorphy for *Adelpha*, also occurring in several closely related outgroup taxa.

31(B). *DHW tornal orange (outer postdiscal series)*: (0) extensive, reaching inner submarginal series along vein 2A and in the middle of cell 2A-Cu2, usually encircling the posterior black spot (Fig. 2Hh); (1) covering the black spot in the posterior half of cell 2A-Cu2 and the posterior half of the inner submarginal series (Fig. 2Ii); (2) less extensive, but reaching vein 2A (Fig. 2Jj); (3) not reaching vein 2A varying to entirely absent (Fig. 2Mm); (4) not extending anteriorly beyond mid cell 2A-Cu2, extending basally to touch the inner postdiscal series (Fig. 2Rr) ($CI_{EW} = 0.19$; $CI_{SACW} = 0.21$).

State 1 is a synapomorphy for the *serpa*-group.

Forewing ventral surface ($CI_{EW} = 0.41$; $CI_{SACW} = 0.39$)

32(B). *VFW discal cell with basal streak*: (0) present (Fig. 3A); (1) absent (Fig. 3B) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).

State 1 is a synapomorphy for the *serpa*-group, which otherwise only occurs in *Adelpha* in *A. argentea* and *A. coryneta*.

33(B). *VFW discal cell with first cell bar*: (0) meeting the cubital vein at a slight angle or smoothly curving (Fig. 3A); (1) sharply angled at the midpoint to merge smoothly into the cubital vein (Fig. 3B); (2) entire bar angled (towards the wing base at the posterior edge of the bar), absent in the anterior half (Fig. 3U); (3) steeply angled (towards the wing base at the anterior edge of the bar) (Fig. 3T) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

34(B). *VFW discal cell with second cell bar*: (0) slightly curving, concave or straight (Fig. 3G); (1) 'S'-shaped (Fig. 3C); (2) convex to strongly inclined, absent in the anterior half (Fig. 3U); (3) forming a circle with the third cell bar (Fig. 3V); (4) irregular (Fig. 3W) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

35(B). *VFW discal cell with second and fourth cell bars*: (0) not touching in the middle (Fig. 3A); (1) touching (Fig. 3N) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

36(B). *VFW discal cell with second and fourth cell bars*: (0) approximately parallel (Fig. 3H); (1) converging to touch posteriorly (Fig. 3I); (2) both concave, touching posteriorly and anteriorly (Fig. 3O); (3) converging posteriorly but not touching (Fig. 3T); (4) converging anteriorly (Fig. 3U) ($CI_{EW} = 0.4$; $CI_{SACW} = 0.4$).

37(B). *VFW discal cell with third cell bar*: (0) present (Fig. 3A); (1) absent (Fig. 3I) ($CI_{EW} = 0.14$; $CI_{SACW} = 0.14$).

38(B). *VFW discal cell with third cell bar*: (0) approximately straight, clearly visible (Fig. 3A); (1) straight, faintly visible (Fig. 3P); (2) 'V'-shaped and often touching second cell bar (Fig. 3C); (3) smoothly concave (Fig. 3L); (4) fused with the dark area between cell bars 3 and 4 (Fig. 3U) ($CI_{EW} = 0.75$; $CI_{SACW} = 1$).

The examination of morphoclines in outgroup species shows that the pale coloration between cell bars 3 and 4 is often reduced, leaving a broad dark band covering this space and cell bar 3. This dark band may also be progressively reduced, as in *Limenitis populi*, visible only as a thin darker line basal of the fourth cell bar, and giving the appearance of the loss of the third cell bar.

39(L). *VFW cell 2A-Cu2 with area between postdiscal band and continuation of first discal cell bar*: (0) entirely pale with a single thin dividing darker line (homologous with third cell bar) (Fig. 3A); (1) white, separated from the postdiscal band by a black line much thinner than the white area (Fig. 3B); (2) with differently coloured basal and distal halves, basal half pale to entirely dark, distal half dark red-brown to dark brown (Fig. 3G); (3) basal half silvery grey, distal half yellow, with a dark dividing line (Fig. 3K); (4) entirely black (Fig. 3R); (5) entirely pinkish-grey (Fig. 3X) ($CI_{EW} = 0.83$; $CI_{SACW} = 0.83$).

40(B). *VFW cell Cu2-Cu1 basal area*: (0) with diffuse or strong pale shading or all dark (Fig. 3B); (1) white at the very base then a separate white spot (Fig. 3C) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

The basal area varies continuously in coloration from light to dark, except in several derived members of the *serpa*-group, in which there is a distinct black basal line, probably homologous with the third cell bar.

41(L). *VFW cell M3-M2 with upper postdiscal band*: (0) present (Fig. 3D); (1) absent (Fig. 3A) ($CI_{EW} = 0.14$; $CI_{SACW} = 0.14$).

42(L). *VFW upper postdiscal band*: (0) ranging from white to silvery grey to lustrous pale cream (Fig. 3D); (1) matt yellowish-brown (Fig. 3Q) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.25$).

In most species the upper postdiscal band is a lustrous colour which differs sharply from the matt browns that often surround the distal edge of the band, except in those species with state 1, in which the latter colour now occupies the entire band.

43(L). *VFW cell Cu2-Cu1 with inner postdiscal series*: (0) present (Fig. 3A); (1) absent (Fig. 3E) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).

- 44(L). *VFW* cell Cu2-Cu1 with outer postdiscal series: (0) present (Fig. 3H); (1) absent (Fig. 3B) ($CI_{EW} = 0.17$; $CI_{SACW} = 0.13$).
- 45(L). *VFW* cell Cu1-M3 with inner postdiscal series: (0) present (Fig. 3A); (1) absent (Fig. 3E) ($CI_{EW} = 0.13$; $CI_{SACW} = 0.1$).
- 46(L). *VFW* postdiscal series anterior of vein M2: (0) present (Fig. 3I); (1) absent (Fig. 3J) ($CI_{EW} = 1$; $CI_{SACW} = 0.5$).

The presence or absence of the inner postdiscal band was treated as separate characters in the two cells Cu2-Cu1 and Cu1-M3, but as a single character in cells anterior of vein M2, because variation appears to be largely independent in the first two cells but strongly correlated in the latter group of cells.

- 47(L). *VFW* cell Cu2-Cu1 with postdiscal band and inner postdiscal series: (0) separate (or with some isolating scales) (Fig. 3H); (1) fused (Fig. 3G) ($CI_{EW} = 0.25$; $CI_{SACW} = 0.2$).
- 48(B). *VFW* cell Cu1-M3 with postdiscal band and inner postdiscal series: (0) separate (or with some isolating scales) (Fig. 3H); (1) fused (Fig. 3G) ($CI_{EW} = 0.17$; $CI_{SACW} = 0.17$).
- 49(L). *VFW* anterior of vein M2 with postdiscal band and inner postdiscal series: (0) separate (at least partially) (Fig. 3B); (1) entirely fused (Fig. 3C) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.2$).
- 50(B). *VFW* cell Cu2-Cu1 inner and outer postdiscal series: (0) separated by a darker line (Fig. 3M); (1) not separated (Fig. 3O) ($CI_{EW} = 0.14$; $CI_{SACW} = 0.09$).
- 51(B). *VFW* cell Cu1-M3 inner and outer postdiscal series: (0) separated by a darker line (Fig. 3L); (1) not separated (Fig. 3M) ($CI_{EW} = 0.13$; $CI_{SACW} = 0.1$).
- 52(B). *VFW* anterior of vein M3 with inner and outer postdiscal series: (0) visibly distinct (Fig. 3L); (1) fused just in cell M1-R5 (Fig. 3P); (2) fused in cells M2-M1 and M1-R5 (Fig. 3H); (3) fused in cells M3-M2 and M1-R5 (Fig. 3S); (4) fused just in cell M3-M2 (Fig. 3Q); (5) fused entirely (Fig. 3M) ($CI_{EW} = 0.42$; $CI_{SACW} = 0.42$).

The rationale for choosing whether to code homologous characters in adjacent cells as discrete or a single character (characters 47–49, 50–52) is the same as that discussed under character 46.

- 53(B). *VFW* inner and outer postdiscal series combined width: (0) similar, or less, in cell M2-M1 than in cell Cu1-M3 (Fig. 3L); (1) greater in cell M2-M1 than in cell Cu1-M3 (Fig. 3H) ($CI_{EW} = 0.25$; $CI_{SACW} = 0.25$).

State 1, in which the fused postdiscal series are expanded in cell M2-M1, has arisen several times within *Adelpha*.

- 54(B). *VFW* with subapical marking (postdiscal series) in cell M1-R5: (0) of similar size and placement relative to the inner submarginal series as in cell M2-M1 (Fig. 3B); (1) much narrower than in cell M2-M1, the distal edge displaced basally from the inner submarginal series (Fig. 3D) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).

State 1 occurs only in species with character 53: 1, and appears to have been derived at least twice in *Adelpha*.

- 55(B). *VFW* outer postdiscal series with dark, intruding interval lines: (0) absent (Fig. 3O); (1) present (Fig. 3F) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

- 56(L). *VFW* distal of postdiscal series in cells Cu1-M3 and M3-M2 with steely grey ground colour, formed by inner submarginal series diffusing basally: (0) absent (Fig. 3O); (1) present (Fig. 3R) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

A grey ground colour occurs in several species at the basal edge of the inner submarginal series, but in two species, *A. argentea* and *A. coryneta*, it is much more extensive, fusing to form a uniform colour across several cells (state 1).

- 57(B). *VFW* inner submarginal series composed of: (0) single spots in each cell (Fig. 3C); (1) paired spots in each cell (Fig. 3D) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- 58(B). *VFW* inner submarginal series: (0) parallel to the margin (Fig. 3D); (1) basally displaced in the middle of the wing (Fig. 3M) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).
- 59(B). *VFW* inner submarginal series: (0) even throughout the wing (Fig. 3G); (1) reduced or absent in cells Cu1-M3 or M3-M2 or both (Fig. 3M) ($CI_{EW} = 0.07$; $CI_{SACW} = 0.06$).
- 60(L). *VFW* cell Cu1-M3 with: (0) some trace of inner submarginal series (Fig. 3M); (1) no trace of inner submarginal series (Fig. 3J) ($CI_{EW} = 0.1$; $CI_{SACW} = 0.09$).

Hindwing ventral surface ($CI_{EW} = 0.46$; $CI_{SACW} = 0.44$)

- 61(B). *VHW* basal area: (0) whitish with the precostal vein lined with brown (Fig. 3Y); (1) with a thin dark line extending from the wing base to the end of the precostal vein, isolating white at the basal angle of the precostal vein (Fig. 3Bb); (2) area basal of the precostal vein entirely orange-brown (Fig. 3Nn); (3) area basal entirely orange, vein lined with black (Fig. 3Ee); (4) entire area and precostal vein pale ground colour (may be some brown shading at the tip precostal but not extending to the wing base) (Fig. 3Pp); (5) costal margin with an even, orange-brown border, just touching the tip of the precostal vein (Fig. 3Qq); (6) broad, dark band extending from the wing base to the margin and covering the distal half of the precostal vein (Fig. 3Rr); (7) broad, dark band covering the precostal vein, vein Sc + R1 to the costal margin, except for a pale area at the wing base costal margin (Fig. 3Ss); (8) pale with a black spot at the wing base and the tip of the precostal vein (Fig. 3Tt) ($CI_{EW} = 0.29$; $CI_{SACW} = 0.25$).

- 62(B). *VHW* discal cell with dark line at base: (0) absent (Fig. 3Pp); (1) present (Fig. 3Y) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

State 1 is an apparent synapomorphy for *Adelpha*, which has been lost in the *serpa*-group.

- 63(B). *VHW* discal cell with first cell bar: (0) not continuing to vein 3A (Fig. 3Bb); (1) continuing to vein 3A (Fig. 3Cc) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

64(L). *VHW discal cell with*: (0) area between cell bars 1 and 2 varying from dark to pale, between 2 and 3 pale (Fig. 3Z); (1) second cell bar absent and area between postdiscal band and first cell bar partially or entirely orange (Fig. 3Cc); (2) orange between cell bars 1 and 2, third cell bar absent (Fig. 3Bb); (3) area between first and second cell bars entirely black, third postcellular red-brown (Fig. 3Oo); (4) cell bars 1 and 2, and 3 and postcellular, merged to form black lines, area between orange (Fig. 3Gg); (5) orange areas between cell bars 1 and 2, and 3 and postcellular, almost merged to form a continuous orange band (Fig. 3Ee) ($CI_{EW} = 0.83$; $CI_{SACW} = 0.83$).

Due to widespread fusion and the loss of pattern between the hindwing discal cell bars, the coloration of the entire area between the first cell bar and the postcellular bar was coded as a single character.

65(L). *VHW discal cell with postcellular bar*: (0) distinct, continuing approximately parallel to the first cell bar into cell M1-Rs (Fig. 3Y); (1) distinct, terminating in or before cell M2-M1, or if extending into M1-Rs angled basally towards the second cell bar (Fig. 3Dd); (2) fused with a dark band lining the basal edge of the postdiscal band, or surrounded by or part of darker ground colour (Fig. 3Gg) ($CI_{EW} = 0.18$; $CI_{SACW} = 0.17$).

66(B). *VHW anal margin with distal edge*: (0) same as ground colour (Fig. 3Y); (1) bordered with a dark line (Fig. 3Z) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.17$).

Several species were coded as equivocal for this character because this area of the wing is uniformly pale brown, making it impossible to assess whether a dark bordering line is present or not.

67(B). *VHW area between anal margin and vein 3A*: (0) shining greenish (Fig. 3Pp); (1) greyish-white (Fig. 3Cc); (2) entirely orange (Fig. 3Uu); (3) entirely yellow-brown (Fig. 3Nn); (4) striped with various colours (Fig. 3Ss); (5) all dark brown (Fig. 3Vv) ($CI_{EW} = 0.6$; $CI_{SACW} = 0.6$).

68(B). *VHW vein 3A with venal stripe*: (0) absent (Fig. 3Pp); (1) present (Fig. 3Gg) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).

A dark stripe lying along vein 3A is interpreted as a 'venal stripe' (*sensu* Nijhout, 1991). State 1 is a synapomorphy for *Adelpha*, also occurring in several outgroup species. However, in all outgroup species there is heavy scaling along all veins, and the state is probably independently derived. The venal stripe is variably heavy, and sometimes appears to be split into two either side of the vein. The configuration of this stripe is coded in characters 69–73.

69(B). *VHW vein 3A with venal stripe*: (0) present, vein 3A white (Fig. 3Dd); (1) vein 3A dark (Fig. 3Gg) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

State 1 is a synapomorphy for derived *Adelpha*.

70(B). *VHW vein 3A with venal stripe*: (0) at anterior side of vein 3A only, vein 3A white (Fig. 3Bb); (1) on vein or on both sides of vein (Fig. 3Gg) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

71(B). *VHW vein 3A with anterior portion of venal stripe*: (0) even throughout or on vein (Fig. 3Ff); (1) heavy, broken at base (Fig. 3Cc); (2) faded and most pronounced in distal half (Fig. 3Y) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

State 1 is a synapomorphy for derived members of the *serpa*-group, whereas state 2 is a synapomorphy for the *alala*-group.

72(B). *VHW vein 3A with posterior portion of venal stripe*: (0) even throughout or on vein (Fig. 3Ff); (1) reduced to a small dash near the base of the vein (Fig. 3Y) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

State 1 is a synapomorphy for the *alala*-group.

73(L). *VHW cell 3A-2A with anterior portion of vein 3A venal stripe*: (0) parallel to vein or absent (if vein dark) (Fig. 3Ff); (1) meeting the anal margin near the middle of cell 3A-2A and extending to the base of the wing (Fig. 3Bb) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

74(B). *VHW cell 3A-2A*: (0) of uniform colour or crossed by bands of colour (Fig. 3Pp); (1) with a dark line between the base of the wing and mid-cell 3A-2A at the anal margin, with varying amounts of darker scaling between the line and vein 2A (Figs 3Y, Z) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.17$).

State 1 is a synapomorphy for *Adelpha*, secondarily lost in a few species. This line is interpreted as the posterior half of a venal stripe along vein 2A (homologous to that along VHW vein 3A, character 68: 1) which has become detached from the vein, as in character 69: 0. One outgroup species, *Pseudacraea lucretia*, has a similar line in the middle of the cell, but this line precisely bisects the cell space, rather than curving towards vein 2A in the basal half of the cell. The line in *Pseudacraea lucretia* is interpreted as a true inter-venal stripe (*sensu* Nijhout, 1991), and thus not homologous. The difference between these two types of line can be clearly seen on the VHW of *A. mesentina*, which has inter-venal stripes parallel to the veins in the anterior half of the wing (Fig. 3Jj).

75(B). *VHW cell 3A-2A with dark line (representing posterior half of vein 2A venal stripe)*: (0) in distal half filling most of the cell (Fig. 3Dd); (1) in middle of the cell or filling the anterior half (Fig. 3Cc); (2) extending along the anal margin to meet vein 3A, isolating a greyish-brown patch at the base of cell 3A-2A (Fig. 3Ll) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

State 0, in which the line is visible as orange coloration filling most of the distal half of the cell, is a synapomorphy for the *serpa*-group.

76(B). *VHW with orange to reddish-brown line extending from wing base to postdiscal band along vein 2A, or anterior edge of vein*: (0) present (Fig. 3Bb); (1) absent (Fig. 3Gg); (2) vein 2A lined with black (Fig. 3Uu) ($CI_{EW} = 0.06$; $CI_{SACW} = 0.06$).

This line is interpreted as the anterior half of the vein 2A venal stripe (see character 76).

77(H). *VHW postdiscal band*: (0) convex (Fig. 3Qq); (1) approximately straight or concave (Fig. 3Pp) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.33$).

- 78(H). *VHW postdiscal band*: (0) distal to the base vein Cu2 (Fig. 3Qq); (1) crossing or touching the base vein Cu2 (Fig. 3Rr) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- 79(L). *VHW ground colour distal of postdiscal band*: (0) with some reddish or brownish shading (Fig. 3Dd); (1) entirely black (Fig. 3Cc) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- Although the ground colour of the VHW is rather variable, in *Adelpha* state 1 has arisen only twice, in *A. melona* and the *serpa*-group.
- 80(B). *VHW inner postdiscal series*: (0) present (at least some trace) (Fig. 3Bb); (1) absent, black ground colour (Fig. 3Cc); (2) absent, reddish-brown ground colour (Fig. 3Ww); (3) absent, yellowish-brown ground colour (Fig. 3Mm); (4) absent, greyish-brown ground colour (Fig. 3Xx); (5) absent, buff ground colour (Fig. 3Tt) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- Loss (or invisibility) of the inner postdiscal series in states 2–5 is unlikely to be homologous, given the differing background colours, so differing colours were coded as discrete characters.
- 81(L). *VHW postdiscal band and inner postdiscal series*: (0) parallel and adjacent (Fig. 3Kk); (1) almost overlapping, postdiscal band absent (Fig. 3Nn) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).
- The postdiscal band or inner postdiscal series is often entirely lost on the hindwing, resulting in equivocal coding for this character.
- 82(B). *VHW inner postdiscal series*: (0) even throughout the wing (Fig. 3Bb); (1) more pronounced near costa (Fig. 3Ff); (2) most pronounced in cell M3-M2 (Fig. 3Hh); (3) most pronounced in cells M2-M1 and M1-Rs (Fig. 3Ii) ($CI_{EW} = 0.23$; $CI_{SACW} = 0.25$).
- 83(H). *VHW outer postdiscal series*: (0) present (at least some trace) (Fig. 3Rr); (1) absent (Fig. 3Ww) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.33$).
- 84(L). *VHW outer postdiscal series in cell Cu2-Cu1*: (0) with outer edge concave (Fig. 3Aa); (1) straight (Fig. 3Ff) ($CI_{EW} = 0.09$; $CI_{SACW} = 0.08$).
- 85(B). *VHW outer postdiscal series*: (0) more pronounced in cell M1-Rs (Fig. 3Dd); (1) even throughout the wing (Fig. 3Ff); (2) much broader in cells Cu2-Cu1, Cu1-M3 and M3-M2 (Fig. 3Nn) ($CI_{EW} = 0.12$; $CI_{SACW} = 0.11$).
- 86(L). *VHW postdiscal series at costa*: (0) separate (Fig. 3Dd); (1) fused (Fig. 3Ff) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.33$).
- 87(B). *VHW with inner submarginal series*: (0) parallel to the distal margin (Fig. 3Z); (1) basally displaced in cell M3-M2 (Fig. 3); (2) basally displaced towards the tornus (Fig. 3Rr) ($CI_{EW} = 0.17$; $CI_{SACW} = 0.17$).
- 88(B). *VHW distal half of wing with dark lines parallel to veins bisecting cell spaces*: (0) absent; (1) present (Fig. 3Jj) ($CI_{EW} = 1$; $CI_{SACW} = 1$).
- 89(L). *VHW outer submarginal series*: (0) pale dashes within a darker ground colour (Fig. 3Gg); (1) entirely replaced by a yellowish to reddish-brown line (may still be present in cell 2A-Cu2) (Fig. 3Nn);

(2) entirely replaced anterior of vein Cu1 by an even red-brown line, present posterior of vein Cu1 as white dashes on a black ground colour (Fig. 3Oo) ($CI_{EW} = 0.4$; $CI_{SACW} = 0.25$).

Male genitalia ($CI_{EW} = 0.67$; $CI_{SACW} = 0.63$)

- 90(B). *Aedeagus with internal, spiny sclerotized pad*: (0) absent; (1) present (Fig. 4B) ($CI_{EW} = 1$; $CI_{SACW} = 1$).
- Synapomorphy for *serpa*-group, also occurring in *Pseudacraea lucretia* and *Neptis hylas*.
- 91(B). *Juxta*: (0) narrow, 'V'-shaped with dorsal setose pads large and at dorsal edge (Fig. 4D); (1) narrow, 'V'-shaped with dorsal setose pads small and below dorsal edge (Fig. 4C); (2) broad, 'V'-shaped with dorsal setose pads large and at dorsal edge (Fig. 4E); (3) an elongate plate lacking setose pads, produced posteriorly near ventral edge (Fig. 4F) ($CI_{EW} = 1$; $CI_{SACW} = 1$).
- State 1 is a synapomorphy for the *serpa*-group.
- 92(B). *Juxta in ventral view with base*: (0) of same width as lateral arms (Fig. 4C); (1) broader than lateral arms (Fig. 4D) ($CI_{EW} = 1$; $CI_{SACW} = 1$).
- 93(L). *Ventral base of gnathos*: (0) smoothly rounded or pointed; (1) base indented forming a 'W'-shape (Fig. 4G) ($CI_{EW} = 1$; $CI_{SACW} = 0.5$).
- 94(H). *Valva*: (0) of approximately even width throughout, not tapering posteriorly (Fig. 4F); (1) with medial dorsal or ventral projections, or both, and tapering posteriorly (Figs 4H–J) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- Despite substantial variation in valva shape, the most basal members of Limenitidini have a valva that is distinctive in lacking medial and ventral projections and being of even width throughout.
- 95(B). *Valva distal spines*: (0) absent (Fig. 4H); (1) present (Figs 4F, I) ($CI_{EW} = 0.09$; $CI_{SACW} = 0.08$).
- 96(B). *Valva distal spines*: (0) in a vertical plane (Fig. 4F); (1) extending laterally in a line (Fig. 4L); (2) laterally scattered (Fig. 4I) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).
- 97(L). *Valva with distal spines*: (0) extending laterally (96: 1), placed at the ventral edge of the valva (Fig. 4K); (1) in the middle of the valva outer edge forming a flat line of spines (Fig. 4L) ($CI_{EW} = 1$; $CI_{SACW} = 1$).
- To avoid coding the same character more than once, where non-applicable characters 96 and 97 were coded as equivocal.
- 98(B). *Valva with spines*: (0) confined to distal tip, pointing posteriorly (Fig. 4M); (1) extending along the ventral edge (Fig. 4N) ($CI_{EW} = 0.25$; $CI_{SACW} = 0.2$).
- 99(B). *Valva with chnicula*: (0) present (Fig. 4O); (1) absent (Fig. 4P) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

State 1 is a synapomorphy for the *serpa*-group, also occurring in more basal outgroup taxa.

100(B). *Chunicula*: (0) triangular, pointed or roundly rectangular (Fig. 4O); (1) a small bump (Fig. 4N); (2) broad and indented in the middle (Fig. 4M) ($CI_{EW} = 0.67$; $CI_{SACW} = 1$).

State 0 includes much non-discrete character variation.

101(B). *Male genitalia with*: (0) valva projecting further posteriorly than uncus (Fig. 4F); (1) uncus projecting further posteriorly, or similar to valva (Fig. 4H) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.33$).

Female genitalia ($CI_{EW} = 0.41$; $CI_{SACW} = 0.37$)

102(B). *Corpus bursae with paired bands of strongly sclerotized signa*: (0) present (Fig. 4Q); (1) absent (Fig. 4R) ($CI_{EW} = 0.25$; $CI_{SACW} = 0.17$).

103(L). *Corpus bursae bands of strongly sclerotized signa*: (0) dorsal (Fig. 4Q); (1) lateral (right hand side) (Fig. 4S); (2) ventral (Fig. 4T) ($CI_{EW} = 0.2$; $CI_{SACW} = 0.2$).

The different apparent position of these bands is due to torsion of the ductus bursae.

104(L). *Corpus bursae bands of strongly sclerotized signa*: (0) elongate (Fig. 4Q); (1) reduced to a small oval (Fig. 4T) ($CI_{EW} = 0.5$; $CI_{SACW} = 0.5$).

105(H). *Appendix bursae*: (0) present (Figs 4U,V); (1) absent (Fig. 4S,T) ($CI_{EW} = 0.33$; $CI_{SACW} = 0.25$).

106(H). *Corpus bursae*: (0) symmetrically rounded or oval, appendix bursae absent (Fig. 4S,T); (1) 'pear'-shaped, narrowing substantially posteriorly, appendix bursae absent (Fig. 4W); (2) appendix bursae present, connected at or near the anterior tip of the corpus bursae (Fig. 4U); (3) appendix bursae present, connected posteriorly of the anterior tip of the corpus bursae (Fig. 4V) ($CI_{EW} = 0.75$; $CI_{SACW} = 0.75$).

Immature stages ($CI_{EW} = 0.88$; $CI_{SACW} = 0.86$)

107(B). *Fifth-instar larva*: (0) green, paler ventrally; (1) dorsally pale brown, ventrally dark green-brown, dorsally mottled with dark green; (2) pale brown except for a large brown patch laterally from the thorax to A2; (3) mixed brown and green with darker brown to green anteriorly descending oblique lateral stripes; (4) finely mottled with light and dark brown and green, forming faintly linear, horizontal markings; (5) grey; (6) black and white chequered with transverse orange bands; (7) whitish, mottled green and brown dorsally from T3-A4 and A6-A8; (8) green, ventrally brown; (9) green, dorsally and ventrally brown; (A) green, mottled darkly on dorsal surface A2-A4; (B) green

with a brown lateral stripe, ventrally pale ($CI_{EW} = 0.83$; $CI_{SACW} = 0.83$).

108(B). *Fifth-instar larva with subdorsal scoli between A2 and A10*: (0) variably present; (1) absent ($CI_{EW} = 1$; $CI_{SACW} = 1$).

109(B). *Fifth-instar larva with subdorsal scoli on A2 arising*: (0) straight from body (Fig. 5A); (1) from a short conical base (height of base similar to width) (Fig. 5B); (2) from a very elongate conical base (height of base much greater than width) (Fig. 5C) ($CI_{EW} = 0.67$; $CI_{SACW} = 0.67$).

110(B). *Fifth-instar larva with lateral spines on subdorsal scoli*: (0) arranged randomly (Fig. 5B); (1) aligned into a single plane (Fig. 5D) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

111(B). *Pupa*: (0) pale silvery grey to pale yellowish-brown; (1) white with a lateral row of large black spots; (2) brown with finer dark brown lines; (3) entirely gold or silver; (4) entirely green; (5) golden brown; (6) dark brown; (7) brown with gold or silver patches; (8) dull maroon; (9) very pale greenish-grey with dorsal and ventral brown stripe on body; (A) mottled whitish with large patches of brown; (B) mottled light and dark brown; (C) green with a brown stripe extending from the ventral base of the cremaster to the base of the dorsal lobe on A2; (D) green with reddish-orange lining dorsal keel and wing keels ($CI_{EW} = 0.77$; $CI_{SACW} = 0.77$).

112(H). *Pupa with anteriorly pointing dorsal projection on A2*: (0) absent (Fig. 5E); (1) present (Fig. 5F–M) ($CI_{EW} = 1$; $CI_{SACW} = 1$).

113(B). *Pupa with dorsal projection on A2*: (0) a small, rounded bump (Fig. 5G); (1) a large, blunt, rounded 'hook', almost touching T2, curved in the middle (Fig. 5H); (2) large, angular, almost touching T2 (Fig. 5I); (3) short, angular (Fig. 5J); (4) rounded (Fig. 5K); (5) a pointed, anterior projection of the dorsal edge only (Fig. 5F); (6) elongate and rounded (Fig. 5L); (7) elongate and angular, almost touching A1-T2 throughout (Fig. 5M); (8) a large, pointed 'hook', curved towards the tip ($CI_{EW} = 0.86$; $CI_{SACW} = 0.75$).

114(B). *Pupal cephalic projections*: (0) very small bumps, almost absent (Fig. 5N); (1) short, broad rectangles (Fig. 5O); (2) flattened, laterally pointing (Fig. 5P); (3) flattened, posteriorly pointing (Fig. 5Q); (4) elongate, closely appressed (Fig. 5R); (5) triangular, blunt (Fig. 5S); (6) thin, elongate, tapering (Fig. 5T); (7) small, rounded lobes, broader at the base than the apex (Fig. 5U); (8) triangular, overlapping plates (Fig. 5V); (9) small, pointed triangles (Fig. 5W); (A) large rounded lobes (Fig. 5X) ($CI_{EW} = 0.88$; $CI_{SACW} = 0.88$).

Appendix 2. Data matrix. Missing data are indicated by '?', data not coded are indicated by '-'; and polymorphic character states are separated by ':'.

	1	5	10	15	20	25	30	35	40	45	50	55	60
		65	70	75	80	85	90	95	100	105	110	114	
<i>P. sylvia</i>	2	0 0 2	-	0 1	? 0 ?	0 0 2	-	0 0 2	3 0 0 3 0 0 -	-	-	-	-
	4	0 ? -	-	0 0	? ? ? ?	0 ?	1 0 0 -	4 ?	0 -	0 -	0 -	3 ?	-
<i>B. austenia</i>	0	1 0 0	0	-	0 0 ? 0 ?	-	0 1 ?	-	? ?	1 -	-	? ?	0 0 0 4 0 ? 0
	4	0 0 -	-	0 1	0 ? ? ?	-	0 0 ?	3 0	0 0 0 0 0 0 -	-	-	-	-
<i>P. lucretia</i>	0	0 1 0	3	-	0 0 ? 0 ?	-	0 1 ?	0 -	4 ?	0 -	4 ?	0 -	1 -
	8	0 0 0	-	1 1	1 1 0 0 -	0 ?	2 0 1 -	5 ?	1 -	-	-	-	-
<i>N. hylas</i>	0	0 0 0	0	-	? 0 ? 0 ?	-	1 1 ?	-	? 0 0 -	-	-	-	-
	7	0 ? -	-	0 4	0 ? ? ? ?	-	0 ?	1 1 -	0 0 -	0 -	0 -	1 -	0 -
<i>B. lorquini</i>	0	0 1 1	0	-	? 0 ? 0 ?	-	0 1 ?	-	? 0 0 0 -	-	-	-	-
	4	0 0 -	-	1 1	1 1 0 0 -	0 ?	2 0 0 -	1 -	? 0 -	0 -	0 -	0 -	0 -
<i>B. weidermeyer</i>	0	0 1 1	0	-	? 0 ? 0 ?	-	0 1 ?	-	? 0 0 0 -	-	-	-	-
	4	0 0 -	-	1 1	1 1 0 0 -	0 ?	2 0 0 -	1 -	? 0 -	0 -	0 -	0 -	0 -
<i>B. archippus</i>	0	1 1 1	0	-	? 0 ? 0 ?	-	0 0 ?	-	? 0 0 0 -	-	-	-	-
	4	0 0 -	-	1 2	1 1 0 0 -	0 ?	0 ?	0 ?	-	0 ?	-	-	-
<i>B. arthemis</i>	0	1 1 1	0	-	? 0 ? 0 ?	-	0 1 ?	-	? 0 0 -	-	-	-	-
	4	0 ? -	-	? 5	? ? ? ?	-	? 2 0 0 -	1 -	? 0 -	0 -	0 -	0 -	0 -
<i>L. camilla</i>	1	0 1 0	0	-	0 0 ? 0 ?	-	0 0 0 -	0 0 -	0 1 0 -	0 -	0 -	0 3 0	0 4 0 0 0 4 -
	5	0 0 -	-	0 0	0 ? ? ? ?	-	0 ?	1 0 0 -	0 -	0 -	0 -	0 -	0 -
<i>L. reducta</i>	1	1 1 0	0	-	? 1 0 0 ?	-	0 1 ?	-	? 0 0 -	-	-	-	-
	4	0 0 -	-	0 1	0 ? ? ? ?	-	0 ?	1 0 0 -	2 ?	0 -	0 -	0 -	0 -
<i>L. populi</i>	2	0 1 0	0	-	? 1 0 0 ?	-	0 1 ?	-	? 0 0 -	-	-	-	-
	5	0 0 -	-	0 0	0 ? ? ? ?	-	0 ?	1 0 0 -	0 -	0 -	0 -	0 -	0 -
<i>A. ranga</i>	1	1 1 0	3	-	0 0 ? 0 ?	-	0 1 ?	-	? 0 0 -	-	-	-	-
	6	0 0 -	-	0 0	0 ? ? ? ?	-	0 ?	1 1 1 -	2 ?	1 -	2 ?	1 -	2 ?
<i>A. asura</i>	1	1 1 0	1	-	? 0 ? 0 ?	-	1 1 ?	-	? 0 0 -	-	-	-	-
	6	0 0 -	-	0 1	0 ? ? ? ?	-	0 ?	1 1 1 -	2 ?	0 -	0 -	0 -	0 -
<i>A. selenophora</i>	2	1 0 0	1	-	? 0 ? 1 0 1 -	-	1 1 ?	-	? ? ? 0 -	-	-	-	-
	6	0 0 -	-	0 1	0 ? ? ? ?	-	0 ?	1 1 1 -	2 ?	0 -	0 -	0 -	0 -
<i>M. lymire</i>	2	0 0 0	0	-	0 1 0 0 ?	-	0 0 0 -	0 0 -	0 0 0 -	-	-	-	-
	4	0 ? -	-	0 0	0 ? ? ? ?	-	0 ?	1 1 0 -	0 0 -	0 -	0 -	0 -	0 -
<i>M. procris</i>	2	1 0 0	0	-	? 0 ? 1 0 -	-	0 0 0 -	0 0 -	0 0 2 -	0 -	0 -	0 -	0 -
	4	0 0 -	-	0 0	0 ? ? ? ?	-	0 ?	1 1 0 -	0 0 -	0 -	0 -	0 -	0 -
<i>S. daraxa</i>	2	0 0 0	0	0	0 ? 1 1 0	0	0 0 0 0	0 0 0	1 0 6 0	0 ?	0 ?	0 ?	0 ?
	4	0 0 0	1	0	0 0 ? ? ? ?	-	0 ?	1 1 0 0	2 0 ?	0 1 ?	0 ?	0 ?	0 ?
<i>S. zulena</i>	1	1 0 0	0	0	0 ? 1 0 0	0	0 0 0 0	0 0 0	1 0 0 0	0 ?	0 ?	0 ?	0 ?
	4	0 0 0	1	0	0 0 ? ? ? ?	-	0 ?	1 1 0 1	0 0 0	0 0	0 0	0 0	0 0
<i>P. zayla</i>	2	0 0 0	0	0	0 ? 1 0 0	0	0 0 0 0	0 0 0	1 1 0 0	0 ?	0 ?	0 ?	0 ?
	4	0 0 0	1	0	0 0 ? ? ? ?	-	0 ?	1 1 0 0	0 0 0	0 0	0 0	0 0	0 0

Appendix 2. continued.

	1	5	10	15	20	25	30	35	40	45	50	55	60
		65	70	75	80	85	90	95	100	105	110	114	
<i>P. dudu</i>	2	100	0	0	1	?	0	00	10	0	0	0	0
	4	000	1	0	?	???	?	1	00	00	0	1	0
<i>A. bredowii</i>	0	011	0	00	1	010	0	0	1	0	2	0	001
	1	000.2	1.2	11	0.10	00?	1	1	0	0	0	1	1
<i>diocles</i>	0	011	-	10	1	0.1110	0	-	1	0	00	0	0
	1	001	2	11	1	0	00?	1	0	1	-	1	?
<i>herbita</i>	?	?	?	?	?	???	0	-	0	?	20	0?	7
	0	001	2	?	1	0	00?	1	0	?	-	1	?
<i>zea</i>	1	111	-	00	0	?	10	0	-	1	?	?	?
	1	001	2	11	1	100	0	1	1	-	-	1	?
<i>parecca</i>	1	111	-	00	1	?	10	0	-	0	1	0	0
	1	011	2	11	1	0	01?	0	1	0	-	1	?
<i>nea</i>	1	111	-	00	0	?	0?	0	-	1	?	?	?
	1	011	2	11	1	0	01?	0	1	0	-	1	?
<i>paraena</i>	1	111	0	00	1	110	0	0	1	?	00	00	2.7
	1	011	2	11	1	0	01?	0	1	0	1	?	?
<i>radiata</i>	1	111	0	00	1	110	0	0	1	?	00	?	7
	1	011	2	11	1	0	01?	0	1	0	1	?	?
<i>serpa</i>	1	111	0	00	1	110	0	0	1	0	00	?	7
	1	011	2	11	1	0	01?	0	1	0	1	?	?
<i>seriphita</i>	1	111	-	00	1	?	10	0	-	0	1	?	?
	1	011	2	11	1	0	01?	0	1	0	00	?	7
<i>hyas</i>	1	111	-	00.1	1	?	10	0	-	1	?	?	?
	1	011	2	11	1	0	01?	0	1	0	-	1	?
<i>alala</i>	0	000	0	00	0	?	0?	0	0	00	00	5	0.1
	0	100	0	01	1	121	0	1	1	0	1	00	0?
<i>aricia</i>	0	000	-	00	0	?	0?	0	-	1	?	?	?
	0	100	0	01	1	121	?	1	1	1	-	0	00
<i>corecya</i>	0	000	-	00	0	?	0?	0	-	1	?	?	?
	0	100	0	01	1	121	?	0.1	-	0	0	1	-
<i>tracta</i>	0	000	0	00	0	?	0?	0	1	?	0	10	1
	0	100	0	01	1	121	0	1	1	0	1	00	0?
<i>pithys</i>	0	000	-	00	0	?	0?	0	-	1	?	?	?
	0	100	0	01	1	121	0	1	1	0	-	0	0?
<i>doryssa</i>	0	000	0	00	0	?	0?	0	1	?	0	00	10
	0	100	0	01	1	121	0	1	1	?	0	00	0.1?
<i>fessonia</i>	1	101	0	00	0	?	10	0	?	0	1	0	?
	0.1	100	1	1	1	0	100	0	1	0	0	0	0.1

Appendix 2. continued.

	1	5	10	15	20	25	30	35	40	45	50	55	60
		65	70	75	80	85	90	95	100	105	110	114	
<i>denialba</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	1	11	1	1	00	0	-	1	0	0	000
<i>epizygis</i>	1	10?	-	00	0	?	0	?	0	2	1	1	0
	0	100	2	11	1	1	100	0	1	0	-	0	000
<i>fabricia</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	-	0	000
<i>capucinus</i>	1	101	0	00	0	?	1	1	0	0	0	0	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>barnesia</i>	1	101	-	00	0	?	1	1	0	0	0	0	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>diazii</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>hesterbergi</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>abia</i>	1	101	-	00	0	?	1	1	0	0	0	0	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>naxia</i>	1	101	-	10	0	?	0	?	0	?	?	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>heraclea</i>	1	101	0	10	0	?	1	1	0	0	0	0	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>atlantica</i>	1	101	-	?	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>malea</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>boeotia</i>	1	101	-	10	0	?	1	1	0	0	0	0	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>amazona</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	2	100	2	11	1	1	100	0	1	0	0	0	000
<i>ximena</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	1	11	1	1	100	0	1	0	0	0	000
<i>delimita</i>	1	101	-	00	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>pollina</i>	1	101	-	00	0	?	1	1	0	0	0	0	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>erotia</i>	1	111	0	00	0	?	1	1	0	0	0	0	0
	1	100	2	11	1	1	100	0	1	0	0	0	000
<i>phylaca</i>	1	101	0	00	0	?	0	?	0	?	0	?	0
	0	100	2	11	1	1	100	0	1	0	0	0	000
<i>messana</i>	1	101	0	00	0	?	0	?	0	?	0	?	0
	1	100	2	11	1	1	100	0	1	0	0	0	000
<i>thesprotia</i>	1	101	0	00	0	?	0	?	0	?	0	?	0
	1	100	2	11	1	1	100	0	1	0	0	0	000

Appendix 2. continued.

	1	5	10	15	20	25	30	35	40	45	50	55	60	
		65	70	75	80	85	90	95	100	105	110	114	114	
<i>mesentina</i>	1	111 0 10 0 0 ?0? 0 0 1 ? 0 10,111 0 1 1 0 1 1 ?0? 3 0 0?101?200 0 0 0 0 11 011 5 ?010???	0	1	1	0	1	1	0	0	0	0	0	
<i>lycorias</i>	3	100 2 ?3 1 1 100 0 1 1 1 ? 00 1? ? 0 0 100 0 0 110?1001 0 0 0 1 0 20 00? 1 11	0	1	1	0	1	1	0	0	0	0	0	
<i>attica</i>	3	100 2 13 1 1 100 0 1 1 1 ? 00 1? ? 0 0 100 0 0 0?101?200 0 ? ? 0.1? ?0? 5 ?010???	0	1	1	0	1	1	0	0	0	0	0	
<i>leuceria</i>	3	104 2 11 1 1 100 0 1 1 0 - 0 00 0 - 1 1 0 2 0 001 2 0 0001?200 0 0 0 0 01 011 5 0000010,10	0	1	1	0	1	1	0	0	0	0	0	0
<i>leucerioides</i>	0	100 1,2 11 1 1 100 0 1 1 1 00 00 1 0 0 0 1 000 0 0 00001?200 0 0 0 0 00 011 5 0000010 0	0	1	1	0	1	1	0	0	0	0	0	
<i>erymanthis</i>	1	101 - 00 0 0 ?0? 0 - 1 ? 0 11 11 0 - 1 0 2 0 0 - 3 0 00001200 0 ? 0 0 0 011 5 0000010 0	0	1	1	0	1	1	0	0	0	0	0	
<i>sichaeus</i>	1	101 - 00 0 0 ?0? 0 - 1 ? 0 11 11 0 - 1 0 2 0 0 - 3 0 00001?200 0 0 0 0 00 011 5 0000011 0	0	1	1	0	1	1	0	0	0	0	0	
<i>rothschildi</i>	0	100 2 11 1 1 100 0 1 1 0 - 0 00 ? - 1 1 0 0 00 0 0 00001?200 0 ? ? 0 0 011 5 0000011 0	0	1	1	0	1	1	0	0	0	0	0	
<i>stilesiana</i>	0	100 1 01 1 1 100 0 0 ? 1 - - 0 00 0 - 0 1 0 1 000 0 0 00001201 0 ? ? 0 0 011 5 0000010 0	0	1	1	0	1	1	0	0	0	0	0	
<i>boreas</i>	1	10? - 00 0 0 ?0? 0 - 1 ? 0 0? ?1 5 - 1 0 2 0 ? - 3 0 00001?201 0 ? ? 0 0 011 5 0000010 0	0	1	1	0	1	1	0	0	0	0	0	
<i>cocala</i>	0	100 1 01 1 1 100 0 1 1 0.1 - - 0 21 0 - 0 1 0 00 0 0 00001?200 0.10 0 0 0 0 011 5 0000011 0	0	1	1	0	1	1	0	0	0	0	0	
<i>felderi</i>	0	100 2 11 1 1 100 0 1 1 0 1 00 0 0 1 0 1 000 0 0 110?0001 1 ? ? 1 0 30 004 1 52	0	1	1	0	1	1	0	0	0	0	0	
<i>leucophthalma</i>	1	101 0 00 0 0 ?0? 0 1 2 0 1 00 0 0 1 ? 0 ?0? 3 0 00001?200 1 0 0 0 11 011 ? 0000?1 1	0	1	1	0	1	1	0	0	0	0	0	
<i>irmina</i>	2	100 2 11 1 1 100 0 1 1 0 - 0 00 0 - 1 1 0 1 010 0 0 110?0001 1 ? ? 1 0 30 00? 1 52	0	1	1	0	1	1	0	0	0	0	0	
<i>saundersii</i>	2	100 1 11 1 1 100 0 1 2 0 - 0 00 0 - 1 1 0 1 010 0 0 0001?200 1 ? ? 0 0 011 ? 0000?1 1	0	1	1	0	1	1	0	0	0	0	0	
<i>lamasi</i>	2	100 1 ?3 1 1 100 0 1 1 1 - 0 01 ? - 1 2 0 1 010 0 0 0001?200 1 ? ? 0 0 11 011 4 00000?1 1	0	1	1	0	1	1	0	0	0	0	0	
<i>salus</i>	2	100 1 ?3 1 1 100 0 0 ? ? 0 - 1 ? 0 31 ? - 0 00 0 - 1 2 0 1 010 0 0 0001?200 1 ? ? 0 0 011 5 0000011 0	0	1	1	0	1	1	0	0	0	0	0	
<i>shuara</i>	0	100 2 11 1 1 100 0 1 1 0 - 0 00 1 - 1 1 1 0?0 0 0 0001?200 0 1 ? 0 0 011 5 0000011 0	0	1	1	0	1	1	0	0	0	0	0	
<i>argentea</i>	3	100 2 11 1 1 100 0 1 1 0 - 0 00 ? - 1 1 ? 1 020 0 0 0001?200 0 1 ? 0 0 011 5 0000011 0	0	1	1	0	1	1	0	0	0	0	0	
<i>coryneta</i>	3	103 2 11 1 1 100 0 1 1 0 - 0 00 0 - 1 0 2 0 - 3 1 0?011?400 0 1 ? ? 0 0 011 5 00010?1 ?	0	1	1	0	1	1	0	0	0	0	0	
<i>jordani</i>	3	103 2 11 1 1 100 0 1 1 0 - 0 10 ? - 1 1 ? 0 20 0 0 0001?400 0 ? ? 0 0 011 5 1001??1 ?	0	1	1	0	1	1	0	0	0	0	0	
	0	100 2 01 1 1 100 0 1 1 0 - 0 00 0 - 1 1 0 1 000 0 0 0001?200 0 0 0 0 0 011 5 0000010 0	0	1	1	0	1	1	0	0	0	0	0	

