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Revised systematics and higher classification of pierid butterflies (Lepidoptera: Pieridae) based on molecular data

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The butterfly family Pieridae comprises approximately 1000 described species placed in 85 genera, but the higher classification has not yet been settled. We used molecular data from eight gene regions (one mitochondrial and seven nuclear protein-coding genes) comprising a total of ~6700 bp from 96 taxa to infer a well-supported phylogenetic hypothesis for the family. Based on this hypothesis, we revise the higher classification for all pierid genera. We resurrect the tribe Teracolini *stat. rev*. in the subfamily Pierinae to include the genera *Teracolus*, *Pinacopteryx*, *Gideona*, *Ixias*, *Eronia*, *Colotis* and most likely *Calopieris*. We transfer *Hebomoia* to the tribe Anthocharidini and assign the previously unplaced genera *Belenois* and *Dixeia* to the subtribe Aporiina. Three lineages near the base of Pierinae (*Leptosia*, *Elodina* and *Nepheronia* + *Pareronia*) remain unplaced. For each of these, we describe and delineate new tribes: Elodinini Braby *tribus nova*, Leptosiaini Braby *tribus nova* and Nepheroniini Braby *tribus nova*. The proposed higher classification is based on well-supported monophyletic groups and is likely to remain stable even with the addition of more data.

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Introduction

The butterfly family Pieridae is a relatively small family of Lepidoptera comprising about 1000 species placed in four subfamilies and 85 genera. Species of Pieridae have long been the subjects of ecological and evolutionary studies (e.g. Watt *et al.* 1977; Wiklund *et al.* 1991, 1996; Stavenga *et al.* 2004, 2006; Kemp *et al.* 2005; Braby 2006; Braby & Trueman 2006; Wheat *et al.* 2007; Braby & Nishida 2010; Dinca *et al.* 2013), but the phylogenetic relationships of the major lineages within the family have only recently been examined in detail (Braby *et al.* 2006). The monophyly of the family is well established (Wahlberg *et al.* 2005; Heikkilä *et al.* 2012), but relationships among the four subfamilies and several genera within the subfamilies have remained uncertain.

The most comprehensive study to date (Braby *et al.* 2006) sequenced one nuclear gene region from representatives of 74 genera and for a subset of 30 of these, an additional two nuclear gene regions and one mitochondrial gene region. They found that the four subfamilies were well-supported monophyletic groups, and their results suggested that Pseudopontiinae were sister to Dismorphiinae, and Coliadinae were sister to Pierinae. The position of Pseudopontiinae has, however, not been stable; for exam-

ple, Heikkilä *et al.* (2012) found, with much lower taxon sampling, that Pseudopontiinae were sister to Pierinae based on one mitochondrial and seven nuclear gene regions. Within Pierinae, Braby *et al.* (2006) found that the tribes Anthocharidini and Pierini were not monophyletic, and thus, they removed a number of genera from these two tribes. Some of these genera were left *incertae sedis*.

Within Pieridae, several studies have been published investigating relationships of species at the genus level (Chew & Watt 2006; Braby & Pierce 2007; Braby *et al.* 2007; Wheat & Watt 2008; Mitter *et al.* 2011; Nazari *et al.* 2011; Müller *et al.* 2013). These studies collectively showed that relationships among supposedly closely related taxa are not that clear and that much additional work remains to be done.

Despite considerable progress in the higher-level systematics of Pieridae, Braby *et al.* (2006) concluded that many issues still require attention. They recommended that future systematic studies of Pieridae concentrate in the following areas: (i) among the higher taxa of Pieridae, deep-level relationships are still poorly resolved, especially the relationships among subfamilies; (ii) within the subfamily Pierinae, relationships of the four major lineages are not well understood, particularly the informal *Colotis* group and the genus *Leptosia*, which may prove to constitute separate tribes, and further investigation is required to establish monophyly and their relationships; and (iii) within the tribe Pierini, relationships of the five major lineages are also poorly resolved, particularly the phylogenetic positions of the genera *Elodina*, *Dixeia* and *Belenois*. Some of these issues may only be resolved by inclusion of data from other gene regions that are able to recover deeper level splits. Here, we use a large molecular data set comprising one mitochondrial and seven nuclear gene regions for a total of ~6700 base pairs to investigate the relationships of higher taxa in the family Pieridae.

Material and methods

A total of 96 taxa of Pieridae were sampled for this study as well as 14 outgroup taxa from the families Nymphalidae, Lycaenidae and Riodinidae taken from a previously published study (Heikkilä *et al.* 2012). The majority of specimens sequenced here are the same individuals as those used in a previous study (Braby *et al.* 2006), with a few specimens collected specifically for this study, and a few taxa for which sequence data were downloaded from NCBI (Table S1). Eight gene regions were sequenced for the pierid samples, including the mitochondrial gene region *cytochrome oxidase subunit I* (COI) and the nuclear gene regions *elongation factor-1α* (EF-1α), *ribosomal protein S5* (RpS5), *carbamoylphosphate synthase domain protein* (CAD), *cytosolic malate dehydrogenase* (MDH), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH), *isocitrate dehydrogenase* (IDH) and *wingless*. PCR and sequencing protocols followed Wahlberg & Wheat (2008). Alignment of gene regions was straightforward, as all are protein-coding genes with a conserved codon structure. These gene regions have been used successfully for studies of other butterfly relationships (Wahlberg *et al.* 2009; Heikkilä *et al.* 2012). Sequences were managed, and data sets created using VoSeq (Peña & Malm 2012).

Partitioning of large data sets is necessary, especially when different gene regions with different mutational dynamics are being used. Traditionally, data sets are partitioned by gene region, sometimes divided into codon positions (Rota 2011). Recently, a new method of partitioning data by relative rates of evolution has been advocated (Cummins & McInerney 2011; Rota & Wahlberg 2012), and here, we compare the two strategies using Bayes factors – a Bayes factor above 10 is considered as significant (Kass & Raftery 1995; Fan *et al.* 2011; Xie *et al.* 2011). The data were first partitioned by GENE, using one subdivision for each gene for a total of eight. The second strategy followed that of Rota & Wahlberg (2012), in which the data were sorted according to relative rates of evolution regardless of gene origin, as calculated by the program TIGER (Cummins & McInerney 2011). The program was set to subdivide all sites into 30 bins of equal ranges of relative rates. Each bin had the following number of sites: bin 1 = 3173, bins 2 to 12 = 0, bin 13 = 3, bin 14 = 1, bin 15 = 0, bin 16 = 50, bin 17 = 3, bin 18 = 21, bin 19 = 9, bin 20 = 15, bin 21 = 53, bin 22 = 39, bin 23 = 174, bin 24 = 137, bin 25 = 169, bin 26 = 352, bin 27 = 474, bin 28 = 544, bin 29 = 1056 and bin 30 = 488. Bins 2 through 23, each of which had fewer than 200 sites assigned to them, were combined with bin 1 (which consists of invariable sites) into one subset, as were bins 24 and 25. As a result, there were seven partitions in the TIGER-partitioned data.

The data were analysed using Bayesian inference and maximum likelihood. The maximum-likelihood analyses were run with RAXML (Stamatakis *et al.* 2008) with 1000 rapid bootstrap replicates and a search for the maximum-likelihood topology on the CIPRES portal. The data were modelled according to the GTR+G model for each partition independently. Bayesian analyses were conducted with MRBAYES 3.2 (Ronquist *et al.* 2012). The analyses were run for 10 million generations sampling every 1000 generations, with the number of independent runs depending on the analysis (minimally two independent runs). The convergence of the likelihood traces of the independent runs was assessed with TRACER v1.5, and the ESS (effective sample size) values were verified to be above 200 for all parameters, which indicates that all parameters were sufficiently sampled to estimate their posterior distributions (Drummond *et al.* 2006).

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Analyses in MRBAYES 3.2 were run twice independently according to the parameters specified above for both the GENE-partitioned data and the TIGER-partitioned data. The model-jumping feature of the program was utilised, and thus, all possible submodels of the GTR family of models were sampled according to their posterior probability (Ronquist *et al.* 2012). The gamma parameter was also included to allow site rate variation. In addition to the phylogenetic analyses, we estimated the marginal likelihoods (MLE) using the stepping-stone sampling method (Xie *et al.* 2011) implemented in MRBAYES 3.2 with the number of generations increased to 20 million. The value of alpha was set to 0.4, and the number of steps was 50 (both of these are the default values in MRBAYES).

Results

Molecular results

The TIGER-partitioned analyses performed the best in both Bayesian analyses (MLE TIGER = –137267.13, MLE GENE = –142444.64) as indicated decisively by Bayes factors (BF = 4497.13 log units, i.e. much higher than 10). Bayes factors represent the ratio between the marginal likelihood estimates from the two partitioning strategies (Fan *et al.* 2011), and generally, values above 10 are considered to be strongly in favour of the model with the higher marginal likelihood (Kass & Raftery 1995; Baele *et al.* 2012). The Bayesian analysis mainly sampled models with five or six parameters (six parameters representing the GTR model) for GENE-partitioned data, while the TIGER-partitioned data showed more variation in sampled models (see Table S2 for details). Specifically, the slowly evolving partitions tended to have two to four parameter models sampled, while the more quickly evolving partitions tended to have five to six parameter models sampled.

However, the different partitioning strategies led to similar topologies, with the main difference being slightly less resolution in the TIGER-partitioned Bayesian analyses (Fig. 1). The unresolved nodes were not supported in any of the analyses (see Fig. S1), suggesting that the TIGER-partitioned analyses were more conservative. We thus focus our discussion of the results on the analyses of the TIGER-partitioned data.

Most relationships within Pieridae were robustly supported, and the subfamilies were found to be monophyletic (Fig. 1). Dismorphiinae were found to be sister to the rest of Pieridae. Within Dismorphiinae, the Palaearctic genus *Leptidea* was sister to the Neotropical genera, which formed a strongly supported clade. The relationships among Pseudopontiinae, Coliadinae and Pierinae were unresolved, although Pseudopontiinae tended to be sister to the other two subfamilies (see Fig. S1). Within Coliadinae, there were two well-supported reciprocally monophyletic groups, which we have designated as the *Eurema*-clade and the *Colias*-clade.

Relationships within Pierinae were somewhat more complex (Fig. 1). Six clades were strongly supported: the *Aporia*-clade, *Pieris*-clade, *Appias*-clade, *Anthocharis*-clade, *Colotis*-clade and the *Nepheronia*-clade. In contrast, placements of the genera *Elodina* and *Leptosia* were not well supported anywhere within Pierinae. Most of the clades mentioned above correspond to previously described tribes and subtribes adopted by Braby *et al.* (2006), but with some interesting differences. We found *Belenois* + *Dixeia* to be sister to the rest of the *Aporia*-clade with very strong support, suggesting that they should be included in Aporiina. We found *Hebomoia* to be sister to the rest of the *Anthocharis*-clade, suggesting that it should be included in Anthocharidini. Not surprisingly, the *Colotis* group proposed by Braby *et al.* (2006) was not supported in our analyses: we found that the genera *Colotis*, *Eronia*, *Ixias*, *Gideona*, *Pinacopteryx* and *Teracolus* form a strongly supported clade, while *Hebomoia* and *Nepheronia* + *Pareronia* were not closely related to these taxa at all. The relationships of the major clades were clear only in the case of the *Appias*-clade being sister to the *Pieris*- and *Aporia*-clades with strong support.

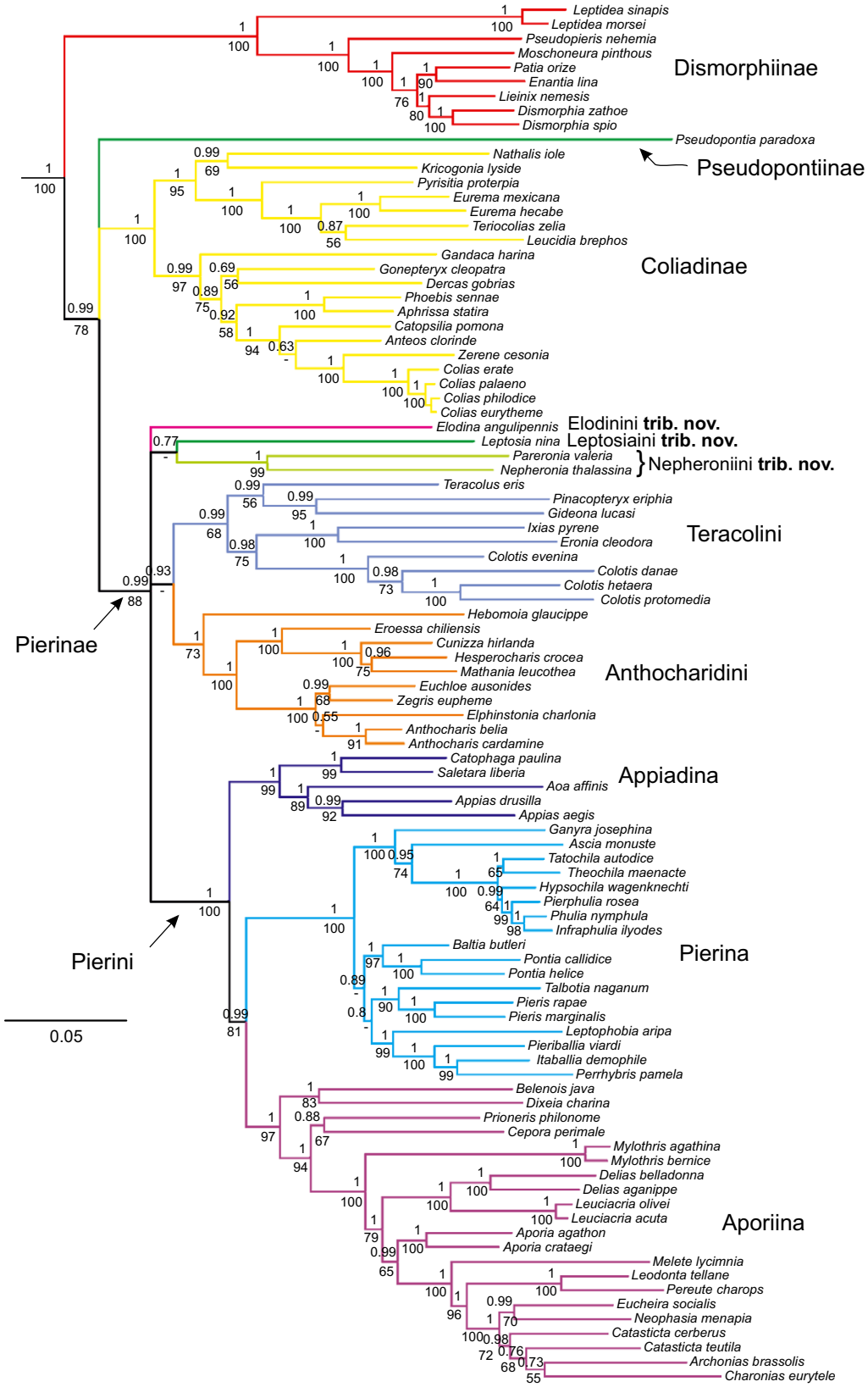
Systematics

A revised higher systematic classification of Pieridae according to the well-supported molecular phylogeny in this study is given in Table 1. The genus *Leptosia* was placed in a group of its own by Braby *et al.* (2006) because it emerged as a somewhat isolated genus with no obvious close relatives and sister to the tribe Pierini. In our analysis, *Leptosia* tended to be sister to the *Nepheronia* group (*Nepheronia* + *Pareronia*), but without strong support. Another genus with no clear affinities was *Elodina* (Braby *et al.* 2006), and in our study, it tended to be sister to the rest of Pierinae in some analyses. Both of these genera plus the *Nepheronia* group are awarded tribal status, as follows.

Elodinini Braby, *tribus nova*
Type genus
Elodina Felder & Felder, 1865

Description

Klots (1933) provided the following wing (Fig. 2A) and male genitalia characters to describe the type genus: forewing with vein R_1 arising from discal cell; vein R_2 stalked on R_{3+4+5} plus M_1 or from upper angle of discal cell; veins R_3 and R_{4+5} completely fused; vein M_1 stalked on R_{3+4+5} about one-third of the distance from end of discal cell to apex; vein M_2 arising from discal cell and connate with R-stem plus M_1 or with a very short middle discocellular (*mdc*); and lower discocellular (*ldc*) very long and recurved.


Leptidea sinapis
Leptidea morsei
Pseudopieris nehemia
Moschoneura pinthous
Patia orize
Enantia lina
Lieinix nemesis
Dismorphia zathoe
Dismorphia spio
Dismorphiinae
Pseudopontia paradoxa
Pseudopontiinae
Nathalis iole
Kricogonia lyside
Pyrisitia proterpia
Eurema mexicana
Eurema hecabe
Teriocolias zelia
Leucidia brephos
Gandaca harina
Gonepteryx cleopatra
Dercas gobrias
Phoebis sennae
Aphrissa statira
Catopsilia pomona
Anteos clorinde
Zerene cesonia
Colias erate
Colias palaeno
Colias philodice
Colias eurytheme
Coliadinae
Elodina angulipennis
Elodinini trib. nov.
Leptosia nina
Leptosiaini trib. nov.
Pareronia valeria
Nepheronia thalassina
Nepheroniini trib. nov.
Teracolus eris
Pinacopteryx eriphia
Gideona lucasi
Ixias pyrene
Eronia cleodora
Colotis evenina
Colotis danae
Colotis hetaera
Colotis protomedia
Teracolini
Hebomoia glaucippe
Eroessa chiliensis
Cunizza hirlanda
Hesperocharis crocea
Mathania leucothea
Euchloe ausonides
Zegris eupheme
Elphinstonia charlonia
Anthocharis belia
Anthocharis cardamine
Anthocharidini
Catophaga paulina
Saletara liberia
Aoa affinis
Appias drusilla
Appias aegis
Appiadina
Pierinae
Pierini
Ganyra josephina
Ascia monuste
Tatochila autodice
Theochila maenacte
Hypsochila wagenknechti
Pierphulia rosea
Phulia nymphula
Infraphulia ilyodes
Baltia butleri
Pontia callidice
Pontia helice
Talbotia naganum
Pieris rapae
Pieris marginalis
Leptophobia aripa
Pieriballia viardi
Itaballia demophile
Perrhybris pamela
Pierina
Belenois java
Dixeia charina
Prioneris philonome
Cepora perimale
Mylothris agathina
Mylothris bernice
Delias belladonna
Delias aganippe
Leuciacria olivei
Leuciacria acuta
Aporia agathon
Aporia crataegi
Melete lycimnia
Leodonta tellane
Pereute charops
Eucheira socialis
Neophasia menapia
Catasticta cerberus
Catasticta teutila
Archonias brassolis
Charonias eurytele
Aporiina
0.05

Hindwing with humeral vein long, nearly reaching margin, straight, sometimes slightly forked at tip; upper discocellular (*udc*) very short; middle discocellular (mdc) short, about one-third the length of lower discocellular (*ldc*), which is strongly curved. Phallus slender, swollen basally, nearly twice as long as combined length of tegumen and uncus, without basal prong; saccus slender, longer than tegumen; tegumen with an articulatory process; uncus short, thick with a pair of dorsal processes extending at base; juxta very small; and valva simple, rounded with no armature.

Diagnosis

In Elodinini, veins R_2 and M_1 of the forewing are both stalked, and the middle discocellular is very short. As in Leptosiaini, veins R_3 and R_{4+5} are completely fused so that there are only three branches of the radial veins, and vein M_2 arises from the upper angle of the discal cell and is usually connate with R-stem plus M_1. Further phylogenetic analysis of morphological characters of Pierinae is needed to establish whether these characters comprise apomorphies or plesiomorphies.

Klots (1933, pp. 216, 230) perceptively concluded that 'In every way *Elodina* is a distinct genus with no near relatives. Its relationships are very doubtful because of the great amount of development that has taken place. In venation it is very highly developed. . .Genitalically considerable reduction has taken place. The author prefers not to even guess at *Elodina*'s ancestry and immediate relationships. . .[it] represents [an] independent line of development.' indicating that he considered the genus to comprise a distinct lineage.

Leptosiaini Braby, *tribus nova*
Type genus
Leptosia Hübner, 1818

Description

Klots (1933) provided the following wing (Fig. 2B) and male genitalia characters to describe the type genus. Liseki & Vane-Wright (2014) also illustrated the wing venation of an African species, *Leptosia alcesta*: forewing with termen and apex very rounded; veins R_1 and R_2 both arising separately from discal cell; veins R_3 and R_{4+5} completely fused; vein M_1 stalked on R_{3+4+5} about one-third to two-fifths of the distance from end of discal cell to apex; vein M_2 arising from discal cell and connate with R-stem plus M_1 or with a very short middle discocellular (*mdc*) or very shortly stalked; lower discocellular (*ldc*) very long and curved. Hindwing with humeral vein short, strongly curved distally; veins M_1 and M_2 connate with discal cell or middle discocellular (*mdc*) very short. Phallus long, slender, nearly straight, with short basal prong distally from base; saccus shorter than tegumen, thin proximally, swollen distally; tegumen long, with a very large articulatory process; uncus short, thick, free part about half its ventral length; juxta very small; valva long, rounded with no armature, and a very heavy sclerotisation in membrane; and subscaphium with a slight sclerotisation.

Diagnosis

In Leptosiaini, the forewing is very rounded, somewhat resembling Pseudopontiinae (Mitter *et al.* 2011), and veins M_1 and M_2 of the hindwing are connate with the discal cell. As in Elodinini, the venation is highly modified, with only three branches of the radial veins (i.e. R_3 and R_{4+5} are completely fused), and vein M_2 arises from the upper angle of the discal cell and is connate with R-stem plus M_1. Further phylogenetic analysis of morphological characters of Pierinae is needed to establish if these characters comprise apomorphies or plesiomorphies.

Klots (1933, pp. 220, 230) remarked that '*Leptosia* has probably been derived from some far-back Pierine stock. In none of its characters does it show any close relationship to any other modern Pieridae, but stands alone. Genitalically it has reached a high point of reduction. In venation, likewise it shows a high degree of specialization. . .*Leptosia* appears to have no close relatives. It probably represents a derivative of a stock that split off far back on the Pierine line of development', indicating that he considered the genus to comprise a distinct 'basal' lineage.

Remarks

The family-group names Leptosiidi Wheeler, 1903 and Leptosiici Kusnezov, 1921 appear to have been based on *Leptosia* Hübner, 1818 but in fact, they were formed under the incorrect assumption that *Leptosia* had been first published in 1819 and included the taxon *Leptosia lathyri* Hübner, 1819, which is a junior subjective synonym of *Leptidea sinapis* (Linnaeus, 1758) (G. Lamas, pers. comm.); that is, the type genus (*Leptosia*) was misinterpreted by both Wheeler (1903, p. 65) and Kusnezov (1921, p. XXIX). *Leptosia* was introduced one year earlier by Hübner (1818, p. 18), and its type species is *Leptosia chlorographa* Hübner, 1818; which is currently regarded as a valid subspecies of *Leptosia nina* (Fabricius, 1793). Therefore, the names introduced by Wheeler (1903) and Kusnezov (1921) are homonymous; they

Fig. 1 A phylogenetic hypothesis of Pieridae genera based on Bayesian inference of eight gene regions partitioned using the TIGER approach. Outgroups have been pruned for clarity. Numbers above branches are posterior probabilities, and numbers below are ML bootstrap values of nodes to the right of the numbers.

Table 1 Revised higher systematic classification of Pieridae based on the results of a phylogenetic analysis of molecular data in this study

Dismorphiinae Schatz, 1886	*Mathania* Oberthür, 1890
Leptidea Billberg, 1820	*Anthocharis* Boisduval, Rambur & Graslin, [1833]
Pseudopieris Godman & Salvin, 1889	*Elphinstonia* Klots, 1930
Moschoneura Butler, 1870	*Euchloe* Hübner, [1819]
Dismorphia Hübner, 1816	*Zegris* Boisduval, 1836
Lieinix Gray, 1832	Pierini Swainson, 1820
Enantia Hübner, [1819]	Appiadina Kusnezov, 1921
Patia Klots, 1933	*Appias* Hübner, [1819]
Pseudopontiinae Reuter, 1896	*Saletara* Distant, 1885
Pseudopontia Plötz, 1870	*Aoa* de Nicéville, 1898
Coliadinae Swainson, 1821	*Udaiana* Distant, 1885
Nathalis Boisduval, 1836	Pierina Swainson, 1820
Kricogonia Reakirt, [1864]	*Baltia* Moore, 1878
Pyrisitia Butler, 1870	*Pontia* Fabricius, 1807
Eurema Hübner, [1819]	*Pieris* Schrank, 1801
Abaeis Hübner, [1819]	*Talbotia* Bernardi, 1958
Teriocolias Röber, 1909	*Leptophobia* Butler, 1870
Leucidia Doubleday, 1847	*Pieriballia* Klots, 1933
Gandaca Moore, 1906	*Itaballia* Kaye, 1904
Gonepteryx [Leach], [1815]	*Perrhybris* Hübner, [1819]
Dercas Doubleday, [1847]	*Glennia* Klots, 1933
Phoebis Hübner, [1819]	*Ganyra* Billberg, 1820
Aphrissa Butler, 1873	*Ascia* Scopoli, 1777
Rhabdodryas Godman & Salvin, 1889	*Reliquia* Ackery, 1975
Prestonia Schaus, 1920	*Tatochila* Butler, 1870
Catopsilia Hübner, [1819]	*Theochila* Field, 1958
Anteos Hübner, [1819]	*Hypsochila* Ureta, 1955
Colias Fabricius, 1807	*Piercolias* Staudinger, 1894
Zerene Hübner, [1819]	*Pierphulia* Field, 1958
Pierinae Swainson, 1820	*Phulia* Herrich-Schäffer, 1867
Elodinini Braby, *tribus nova*	*Infraphulia* Field, 1958
Elodina Felder & Felder, 1865	Aporiina Chapman, 1895
Leptosiaini Braby, *tribus nova*	*Belenois* Hübner, [1819]
Leptosia Hübner, [1818]	*Dixeia* Talbot, 1932
Nepheroniini Braby, *tribus nova*	*Cepora* Billberg, 1820
Nepheronia Butler, 1870	*Prioneris* Wallace, 1867
Pareronia Bingham, 1907	*Mylothris* Hübner, [1819]
Teracolini Reuter, 1896 *stat. rev.*	*Delias* Hübner, [1819]
Colotis Hübner, [1819]	*Leuciacria* Rothschild & Jordan, 1905
Eronia Hübner, [1823]	*Aporia* Hübner, [1819]
Ixias Hübner, [1819]	*Melete* Swainson, [1831]
Teracolus Swainson, [1833]	*Pereute* Herrich-Schäffer, 1867
Calopieris Aurivillius, 1899	*Leodonta* Butler, 1870
Pinacopteryx Wallengren, 1857	*Neophasia* Behr, 1869
Gideona Klots, 1933	*Eucheira* Westwood, 1834
Anthocharidini Scudder, 1889	*Catasticta* Butler, 1870
Hebomoia Hübner, [1819]	*Archonias* Hübner, [1831]
Eroessa Doubleday, 1847	*Charonias* Röber, 1908
Cunizza Grote, 1900	
Hesperocharis C. Felder, [1863]	

are also junior synonyms of Leptidiinae [sic] Grote, 1897, which in turn is a junior subjective synonym of Dismorphiden [sic] Schatz, 1886 (G. Lamas, pers. comm.).

Given these nomenclatural issues surrounding the family-group name for *Leptosia*, we refrain from proposing the name 'Leptosiini' because it might be regarded as a homonym of Leptosiidi Wheeler, 1903; or Leptosiici Kusnezov, 1921;. Therefore, we propose the tribe as Leptosiaini following articles 29.4.2 and 29.3.3 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature (1999), treating the stem of *Leptosia* as an arbitrary combination of letters, presumably based on the Greek 'leptos', which means thin or delicate.

Nepheroniini Braby, *tribus nova*
Type genus
Nepheronia Butler, 1870

Description

Klots (1933) listed 13 morphological character states concerning the head, leg, wing (Fig. 2C) and male genitalia that were in common to both *Nepheronia* and *Pareronia*; van Son (1949) provided additional antennal and wing venation characters by which to diagnose *Nepheronia*: head with antenna shorter than half the length of forewing costa, with gradual but distinct and somewhat flattened club; third segment of labial palp short and oval shaped. Tarsus with pulvillus and paronychia. Forewing with five radial veins present, of which branches R_3, R_4 and R_5 are stalked; vein R_1 arising from discal cell two-thirds from base; vein R_2 arising from nearer to R_1 than to upper angle of discal cell; vein M_1 arising from, or from very near, upper angle of discal cell and connate with R-stem (R_3+R_4+R_5); and middle discocellular (*mdc*) more than half the length of lower discocellular (*ldc*). Hindwing with humeral vein long and usually curved distally from near its base; middle discocellular (*mdc*) from half to the same length as lower discocellular (*ldc*); and veins Rs, M_1 and M_2 arising separately from discal cell. Phallus thick, a little longer than combined length of tegumen and uncus, gently recurved, without basal prong; saccus thick, about as long as tegumen; tegumen long with a large articulatory process; and valva with a simple distal process.

Diagnosis

Klots (1933) used 16 morphological characters to describe the genera *Nepheronia*, *Pareronia* and *Eronia*. Of these, the states for three characters are uniquely shared with *Nepheronia* and *Pareronia*: (i) middle discocellular (*mdc*) of both wings from half or more than half the length to the same length as lower discocellular (*ldc*) (in *Eronia*, *mdc* is shorter, being less than half the length as *ldc*); (ii) valva with a simple distal process (in *Eronia*, the valva is rounded without a distal process); and (iiii) phallus thick, a little longer than combined length of tegumen and uncus and without a basal prong (in *Eronia*, the phallus is stout and longer, being nearly twice the length of tegumen–uncus, and has a

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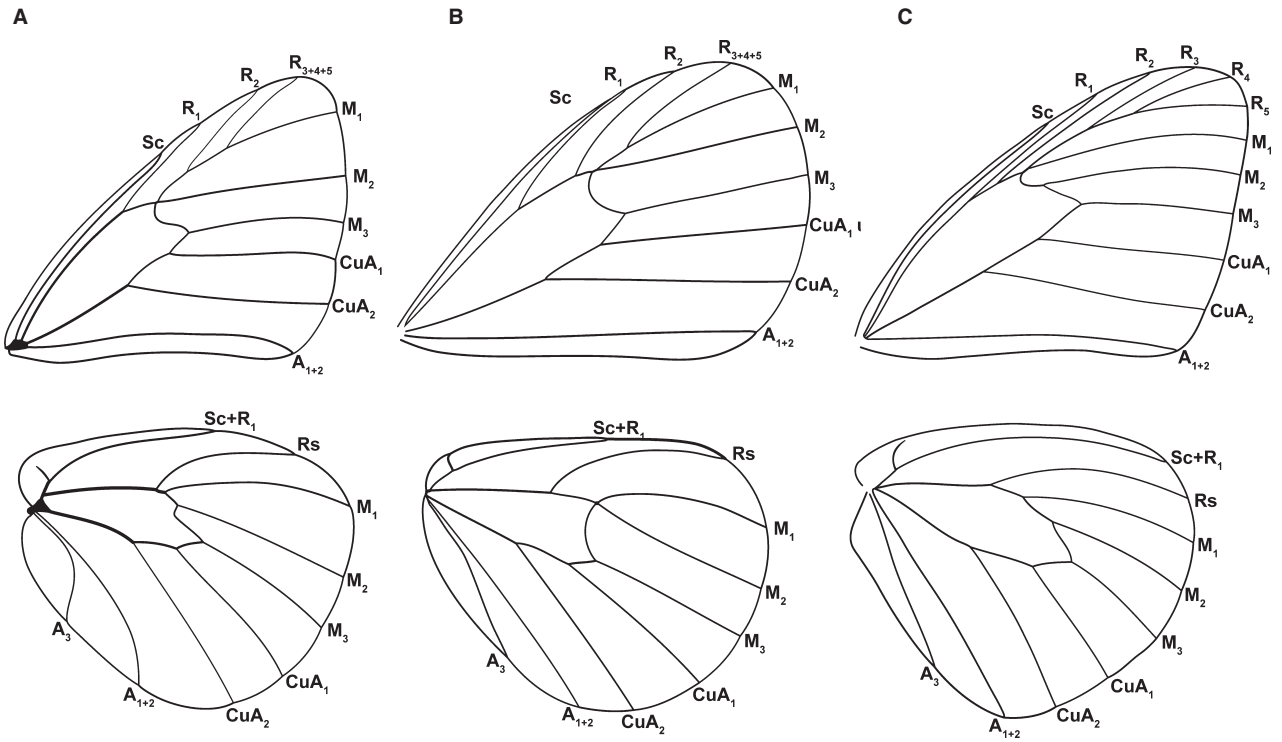

Fig. 2 Wing venation of Pieridae: —A. *Elodina perdita* (modified from De Baar & Hancock 1993); —B. *Leptosia nina* (modified from Corbet & Pendlebury 1992); and —C. *Pareronia anais* (modified from Corbet & Pendlebury 1992).

basal prong). The combination of these three characters appears to be unique to Nepheroniini, although each character on its own may not be diagnostic; for example, the character states for the relative length of the hindwing discocellulars and the posterior shape of the male valva are both shared with at least two genera in Teracolini (*Teracolus*, *Gideona*). The form of the phallus may comprise a synapomorphy for the tribe: although it is similar in profile to several genera of Coliadinae in that the basal prong is absent, the phallus of *Nepheronia* and *Pareronia* is shorter, somewhat straighter (gently recurved) and broader than in that group. There may be additional differences in the form of the saccus, although Klots did not provide complete comparative data for this character. Further study and comparative analysis of morphological characters of Nepheroniini and related taxa in Pierinae, especially the tribes Teracolini, Anthocharidini, Leptosiaini and Elodinini, are needed to assist in differentiating the tribe.

Klots (1933) recognised the close relationship between *Nepheronia* and *Pareronia* based on a suite of morphological characters, placing them in an informal 'primitive' group of pierines that he termed the Eroniine genera or Eroniae, which he regarded to be related to Coliadinae phylogenetically through retention of several ancestral traits (e.g. five radial veins of the forewing, short third segment of the labial palpus, swollen wing case of the pupa); however, this group also included the genus *Eronia*, which Klots considered to be very closely related to *Nepheronia* and *Pareronia*. In our analysis, however, *Eronia* was more distantly related to these genera and emerged sister to *Ixias* within Teracolini. Nepheroniini are therefore considered to comprise only two genera, *Nepheronia* and *Pareronia*.

Discussion

The phylogenetic relationships of the major lineages of Pieridae that we have inferred based on eight gene regions are broadly similar to a previous systematic hypothesis of the family (Braby *et al.* 2006). There are, however, several major differences that have implications for the classification of the family and for understanding the evolutionary history of the group. With regard to the relationships of the subfamilies, the most significant differences are in the placement of Dismorphiinae, which emerges as the sister taxon to the rest of Pieridae, and of Pseudopontiinae, which are more closely related to Coliadinae and Pierinae. In previous analyses, Dismorphiinae were usually found to be sister to Pseudopontiinae (e.g. Braby *et al.* 2006).

Relationships within the subfamily Dismorphiinae, of which all genera were sampled, are clear (Fig. 1). The Neotropical genera form a strongly supported monophyletic group sister to the Palaearctic genus *Leptidea*. This compact, well-defined subfamily comprises approximately

50 species that are well known for taking part in mimicry of other butterflies in the Neotropics, particularly species of Nymphalidae.

Relationships within the subfamily Coliadinae are also relatively clear. We found two well-supported reciprocally monophyletic groups in the subfamily. One clade (the *Colias*-clade) comprises the genera *Gandaca*, *Gonepteryx*, *Dercas*, *Phoebis*, *Aphrissa*, *Catopsilia*, *Anteos*, *Zerene* and *Colias*. This clade most likely also includes the genera *Prestonia* and *Rhabdodryas*, which were not sampled in this study. The second clade (the *Eurema*-clade) comprises the divergent genera *Kricogonia* and *Nathalis* plus the genera *Pyrisitia*, *Teriocolias*, *Leucidia* and *Eurema* (as well as *Abaeis*, not sampled here), which may be better treated under a single cosmopolitan genus *Eurema sensu lato*.

Relationships within the subfamily Pierinae differ to some extent from Braby *et al.* (2006), largely because of good support for the placement of several problematic genera, but as in Braby *et al.* (2006), the basal nodes of Pierinae are largely unresolved. All the major clades are, however, recovered in our analyses with strong support, allowing us to suggest a stable classification for the subfamily. Traditionally, the subfamily was divided into two tribes, Anthocharidini and Pierini (Braby 2005), although Braby *et al.* (2006) were not able to confidently place four genera (*Leptosia*, *Elodina*, *Dixeia* and *Belenois*), which were left *incertae sedis*. In addition, Braby *et al.* (2006) subdivided Pierini into several subtribes, *viz*: Pierina, Appiadina and Aporiina, and recognised an informal group of genera (the *Colotis* group). Our results support this arrangement to some extent, with five strongly supported clades as well as three independent lineages comprising the tribes Nepheroniini, Elodinini and Leptosiaini.

The *Colotis* group of genera was proposed by Braby *et al.* (2006), but it was not accorded formal higher-level status because support for monophyly was weak. Our analyses clearly show that it is polyphyletic, with the constituent genera distributed among three clades. The core taxa (*Teracolus*, *Pinacopteryx*, *Gideona*, *Ixias*, *Eronia*, *Colotis*) do comprise a monophyletic group, and presumably *Calopieris* (not sampled in this study) belongs here as well, but *Hebomoia*, *Nepheronia* and *Pareronia* are more distantly related and have affinities elsewhere. Because the core taxa do form a strongly supported clade, we accord them tribal status Teracolini *stat. rev.* introduced by Reuter (1896).

Hebomoia, previously placed in the *Colotis* group, emerges as sister to Anthocharidini with strong support, and we thus place it in the tribe, as was initially proposed by Klots (1933) in his classic morphological revision of the higher classification of the family. The genus is restricted to the Oriental Region, so its placement in Anthocharidini has implications for the biogeography of the tribe, which otherwise is restricted to the Palaearctic, Nearctic and Neotropical regions. Our results suggest that Anthocharidini and Teracolini are sister groups, although the support for this arrangement is weak. Within Anthocharidini, two reciprocally monophyletic groups uncovered in Braby *et al.* (2006) are evident, the Neotropical *Hesperocharis* group (Braby & Nishida 2007) and a Holarctic *Anthocharis* group comprising *Euchloe*, *Zegris*, *Anthocharis* and *Elphinstonia*.

The other pair of genera, *Nepheronia* from Africa and Madagascar and *Pareronia* from the Oriental and Australian Regions, also previously placed in the *Colotis* group, appear to comprise an independent lineage with no close affiliations to other genera in the subfamily Pierinae. The two taxa form a strongly supported group based on molecular data. Klots (1933) also considered them to be very closely related in his higher classification based on morphological characters, and he suggested they occupied a 'primitive' phylogenetic lineage within the subfamily. For these reasons, we have placed them in a tribe of their own, Nepheroniini.

Another lineage without clear affinities is the monotypic tribe Elodinini, which was weakly placed as sister to the rest of Pierinae in some analyses. Its sole genus *Elodina* had good coverage of gene regions sequenced (6 out of 8 gene regions), and thus, the lack of resolution is likely to stem from lack of informative characters rather than missing data. Elodinini are relatively species rich (ca. 25 species), and thus, increasing sampling of species may help resolve its position. The tribe is restricted to the Australasian Region (including Wallacea), and its position as sister to the rest of Pierinae, should this indeed be the case, may have important historical biogeographic implications.

Leptosia is another isolated genus, which we have placed in a tribe of its own, Leptosiaini. The genus comprises nine species distributed in the Old World tropics, with the majority of species in Africa. One species, *Leptosia nina*, occurs in the Oriental and Australian Regions, and another, *Leptosia lignea*, is restricted to Wallacea. Relationships of the species in this genus would also shed light on the historical biogeography of Pierinae.

The remaining three well-supported clades (the *Appias*-, *Pieris*- and *Aporia*-clades) were treated as subtribes of the tribe Pierini by Braby *et al.* (2006). Appiadina were relatively poorly sampled in this study, but our results corroborate Braby *et al.* (2006) with regard to the paraphyly of *Appias*. This has been discussed at some length previously (Yata *et al.* 2010), and one solution is to synonymise the genera *Saletara*, *Aoa* and *Udaiana* under a single genus *Appias sensu lato* or to treat several of the subgenera of *Appias* as full genera. A more comprehensive taxon sampling of the subtribe, including *Udaiana* and the subgenus *Appias* (*Appias*), and the inclusion of both molecular and morphological data are needed to test these hypotheses before making formal systematic changes.

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The subtribe Pierina is divided into two reciprocally monophyletic groups, which are consistently recovered in all analyses – a New World clade comprising *Ganyra*, *Ascia* and the *Tatochila* group of genera (many of which are restricted to the high Andes of South America), and the more widely distributed clade comprising *Baltia*, *Pontia*, *Pieris*, *Talbotia* and the Neotropical genera *Leptophobia*, *Pieriballia*, *Itaballia* and *Perrhybris* (Fig. 1). The high altitude genera *Reliquia* from Colombia and *Piercolias* from Peru and Bolivia probably belong to the former clade, while *Glennia* from southern Brazil presumably belongs to the latter clade.

Within Aporiina, the relationship of *Aporia* to the *Delias* group and the *Catasticta* group was unresolved in Braby *et al.* (2006, 2007). In our analyses, *Aporia* is sister to the *Catasticta* group with strong support. In addition, we find the position of *Belenois* + *Dixeia* as sister to the rest of Aporiini to be strongly supported; thus, we assign them to this subtribe.

In summary, our analyses of eight gene regions have clarified the higher systematics of Pieridae to an extent that we can propose a well-supported revised classification for the group (Table 1). Analysis and integration of morphological characters (Wahlberg & Nylin 2003; Heikkilä *et al.* 2012), especially from immature stages, may continue to improve resolution. In particular, an analysis of morphological characters can aid in the recognition of synapomorphies to help diagnose clades and further define the higher taxa proposed in this work.

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Supporting Information

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

Fig. S1. Maximum likelihood topologies resulting from the analyses of the by GENE and by TIGER partitioned data, as well as the Bayesian inference result from the analysis of the by GENE partitioned data.

Table S1. Specimens sequenced in this study along with GenBank accession numbers

Table S2. Sampled models in the Bayesian analyses of the two data sets.