Cladistics

Cladistics 24 (2008) 642–676

10.1111/j.1096-0031.2008.00218.x

Phylogenetic relationships of subfamilies and circumscription of tribes in the family Hesperiidae (Lepidoptera: Hesperioidea)

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Accepted 10 January 2008

Abstract

A comprehensive tribal-level classification for the world's subfamilies of Hesperiidae, the skipper butterflies, is proposed for the first time. Phylogenetic relationships between tribes and subfamilies are inferred using DNA sequence data from three gene regions (*cytochrome oxidase subunit I-subunit II*, *elongation factor-1α* and *wingless*). Monophyly of the family is strongly supported, as are some of the traditionally recognized subfamilies, with the following relationships: (Coeliadinae + (“Pyrginae” + (Heteropterinae + (Trapezitinae + Hesperiinae)))). The subfamily Pyrginae of contemporary authors was recovered as a paraphyletic grade of taxa. The formerly recognized subfamily Pyrrhopyginae, although monophyletic, is downgraded to a tribe of the “Pyrginae”. The former subfamily Megathyminae is an infra-tribal group of the Hesperiinae. The Australian endemic *Euschemon rafflesia* is a hesperiid, possibly related to “Pyrginae” (Eudamini). Most of the traditionally recognized groups and subgroups of genera currently employed to partition the subfamilies of the Hesperiidae are not monophyletic. We recognize eight pyrgine and six hesperiine tribes, including the new tribe Moncini.

The family Hesperiidae, commonly known as “skippers” or “skipper butterflies”, includes around 4000 species (Bridges, 1993), currently distributed among 567 genera (Appendix 1). Compared with our understanding of all other butterfly families, our knowledge of hesperiid geographical distributions, immature stages, larval foodplants, and phylogenetic relationships remains poor (Warren, 2000; Wahlberg et al., 2005b). Furthermore, there is no consensus on the taxonomic status of various skipper groups, or on the overall limits of the family. For example, the Megathyminae (or “giant skippers”) have variously been considered to represent a family (e.g. Freeman, 1969b), subfamily (e.g. Mielke, 2004, 2005), or a specialized group of genera within the subfamily Hesperiinae (e.g. Ackery et al., 1999). Similarly, the Australian endemic *Euschemon rafflesia*, which, like no other butterfly, possesses a frenulum and retinaculum in the male, has often been considered to be a “moth” (e.g. Butler, 1870; Scudder, 1875; Watson, 1893), or to represent a family-group taxon within the Hesperiidae (e.g. Mabille, 1876; Janse, 1925; Voss, 1952), while some authors have placed it in the Pyrginae (e.g. Evans, 1949).

About 130 years ago, Adolph Speyer (1877) wrote, “A systematic treatment of the Hesperidae [*sic*] is a very difficult task, and, according to my opinion, can only be accomplished with reference to the whole known family, in all parts of the world…” Despite these sage words, the most recent efforts to reconcile the hesperiid fauna of the world in a uniform systematic arrangement were attempted over 100 years ago (Watson, 1893; Mabille, 1903–1904). All systematic treatments of the Hesperiidae since Mabille (1903–1904) have been regional in nature, save the cosmopolitan exemplar study by Voss (1952), which included a limited sample of 54 species.

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William Harry Evans' (1937, 1949, 1951, 1952, 1953, 1955) monumental series of monographs represents the most recent revision of the world's fauna of Hesperiidae, although he proposed somewhat independent classification schemes for each of the world's regions. Evans arranged phenotypically similar genera into informal groups to aid in their identification, but rarely hypothesized relationships among groups in the same subfamily distributed in different parts of the world. Although there have been some modifications to Evans' classification (see Appendix 1), his taxonomic system remains largely intact in current treatments of the group. As a result, Hesperiidae is the only family of butterflies without a widely accepted tribal-level classification for all of the major subfamilies (Ackery et al., 1999; Lamas, 2004; Mielke, 2005). As noted by Voss (1952), the skippers' "remarkable uniformity of structure leaves us with so little upon which to base sound distinctions that we often are forced to consider significant any trivial character that appears to be a fairly consistent criterion to characterize a group". Indeed, few morphological synapomorphies have been identified that can readily characterize any subfamily of skippers (Ackery et al., 1999), and there is no general consensus on the composition of or relationships among the various subfamilies (de Jong et al., 1996).

Considering the recent progress in understanding the higher-level systematics of other groups of Lepidoptera (e.g. Weller et al., 1994; Brower, 2000; Regier et al., 2000, 2002; Wiegmann et al., 2000; Caterino et al., 2001; Bucheli and Wenzel, 2005; Wahlberg et al., 2005a,b; Braby et al., 2006; Brower et al., 2006; Peña et al., 2006), it is clear that molecular characters can be useful in delineating higher-level taxa and determining relationships. We agree with Larsen (2005), who noted for the Hesperiidae, "A molecular study to assist in the redefinition of subfamilies, tribes, and genera – and not least the relationships within the family worldwide – would be a worthwhile exercise".

In the present study we test the monophyly of the most recent circumscriptions of the subfamilies of the Hesperiidae, as well as Evans' generic groupings within each subfamily. We endeavour to delineate tribes within the major subfamilies, and determine relationships among tribes and subfamilies of the Hesperiidae. We also aim to gain preliminary insights into certain historically controversial genus-level relationships. Hesperiidae is currently divided into seven subfamilies, namely Coeliadinae, Pyrrhopyginae, Pyrginae, Heteropterinae, Trapezitinae, Hesperiinae and Megathyminae (see Table 1), which include a total of 567 genera (see Appendix 1). Some recent authors (e.g. Atkins, 2005) recognize an eighth subfamily, Euschemoninae, while other authors treat the Heteropterinae (e.g. Bridges, 1993; Pyle, 2002) or Megathyminae (e.g. Ackery et al., 1999; Opler and Warren, 2002) as subordinate taxa of the Hesperiinae. Evans divided the Pyrrhopyginae, Pyrginae and Hesperiinae into a total of 28 generic groups, a few of which have since been modified and given formal recognition at the tribal or subfamily level (e.g. Higgins, 1976; Mielke, 2001). Evans further divided nine of his generic groups into 38 subgroups, for a total of 58 suprageneric taxa. We have sampled one or more members from all but three of Evans' groups and subgroups, and two or more members from all but ten of these (excluding monotypic subgroups), allowing us to make a preliminary assessment of the monophyly of most of Evans' suprageneric hypotheses (see Appendix 1), and to evaluate the naturalness of these groups as a basis for a phylogenetic tribal classification. Our hypothesis of relationships is based upon DNA sequences from three gene regions: a contiguous region of mitochondrial *cytochrome oxidase subunits I* and *II* (*COI-COII*), and nuclear *elongation factor-1*α (*EF-1*α) and *wingless*.

Materials and methods

Taxon sampling

Adult butterflies were sampled with aerial nets in the field, by the authors and various colleagues. Specimens were preserved in 85–100% ethanol, with wings removed prior to submersion, or were preserved dry, in glassine envelopes. The species sampled and their collection localities are listed in Appendix 2. A total of 209 species in 198 genera are included in the combined analysis of three genes, discussed below, representing about 35% of the world's skipper genera (*sensu* Ackery et al., 1999; Mielke, 2001, 2004, 2005; see Table 1, Appendix 1). Partial (two gene segments) or complete data were obtained for 22 additional genera and species (marked with an asterisk in Appendix 1), which were not included in the final combined analysis but were included in alternative analyses and are discussed below. Sequences for all taxa are new, except for outgroups and five skipper species, which were published in Wahlberg et al. (2005a). Five outgroup species (see Appendix 2) were selected, one from each family of the Papilionoidea, the putative sister clade to the Hesperioidea (Wahlberg et al., 2005a). Sequences for the outgroup species were obtained from GenBank.

Laboratory protocols

Total genomic DNA was extracted from individual butterflies, by using a standard phenol–chloroform extraction protocol (Brower, 1994, 2000) or Qiagen's DNEasy extraction kits (Qiagen, Venlo, the Netherlands) according to the manufacturer's instructions. We extracted DNA from the thorax of specimens preserved in ethanol, or from two legs of dried butterflies. Vouchers consist of vials of DNA suspended in

Table 1
Traditional and revised family-level classifications of Hesperiidae. Left column represents the classification proposed by Evans and subsequent authors, as detailed in Appendix 1. Right column represents the classification proposed in this paper. Dashes prior to names indicate the following taxonomic status: 1 = family-level name; 2 = subfamily-level names; 3 = tribal names; 4 = subtribal names; 5 = subjective junior synonyms; 6 = unavailable names

Previous suprageneric classification of the Hesperiidae*	Revised suprageneric classification of the Hesperiidae
HESPERIOIDEA Latreille, 1809	**HESPERIOIDEA** Latreille, 1809
- - - - - - ↕ *Netrocera* Haase, 1891	- - - - - - ↕ *Netrocera* Haase, 1891
- - - - - - ↕ *Grypocera* Karsch, 1893	- - - - - - ↕ *Grypocera* Karsch, 1893
- - - - - - ↕ *Urbicolides* Tutt, 1905	- - - - - - ↕ *Urbicolides* Tutt, 1905
- **HESPERIIDAE** Latreille, 1809	- **HESPERIIDAE** Latreille, 1809
- - - - - - ↕ *Diorthosia* Rafinesque, 1815	- - - - - - ↕ *Diorthosia* Rafinesque, 1815
- - - - - - ↕ *Erynnidae* Hampson, 1918	- - - - - - ↕ *Erynnidae* Hampson, 1918
- - **COELIADINAE** Evans, 1937	- - **COELIADINAE** Evans, 1937
- - - - - - ↕ *Ismenini* Mabille, 1878	- - - - - - ↕ *Ismenini* Mabille, 1878
- - - - - - ↕ *Rhopalocamptinae* Evans, 1934	- - - - - - ↕ *Rhopalocamptinae* Evans, 1934
- - **PYRRHOPYGINAE** Mabille, 1877	- - **PYRGINAE** Burmeister, 1878
- - - - - = **Tamyrididae** Burmeister, 1878 (emended)	- - - - - - ↕ *Hesperides* Scudder, 1874
- - - **OXYNETRINI** Mielke, 2001	- - - **EUDAMINI** Mabille, 1877; **confirmed status**
- - - **PASSOVINI** Mielke, 2001	- - - - - = **Telegonidae** Burmeister, 1878
- - - **PYRRHOPYGINI** Mabille, 1877	- - - - - = **Euschemonidae** Kirby, 1897
- - - **ZONIINI** Mielke, 2001	- - - - - = **Phocidinae** Tutt, 1906
- - **PYRGINAE** Burmeister, 1878	- - - - - = **Achalarinae** Swinhoe, 1912
- - - - - - ↕ *Hesperides* Scudder, 1874	- - - - - = **Urbanini** Orfila, 1949
- - - **EUDAMINI** Mabille, 1877	- - - **PYRRHOPYGINI** Mabille, 1877; **reinstated status**
- - - - - = **Telegonidae** Burmeister, 1878	- - - - **Pyrrhopygina** Mabille, 1877; **new status**
- - - - - = **Euschemonidae** Kirby, 1897	- - - - - = **Tamyrididae** Burmeister, 1878 (emended)
- - - - - = **Phocidinae** Tutt, 1906	- - - - **Oxynetrina** Mielke, 2001; **new status**
- - - - - = **Achalarinae** Swinhoe, 1912	- - - - **Passovina** Mielke, 2001; **new status**
- - - - - = **Celaenorrhinae** Swinhoe, 1912	- - - - **Zoniina** Mielke, 2001; **new status**
- - - - - = **Urbanini** Orfila, 1949	- - - **TAGIADINI** Mabille, 1878; **confirmed status**
- - - **PYRGINI** Burmeister, 1878	- - - - - = **Coladeniina** Koçak & Seven, 1997; **new status**
- - - - - = **Achlyodidae** Burmeister, 1878	- - - - - = **Odontoptilina** Koçak & Seven, 1997; **new status**
- - - - - = **Antigonini** Mabille, 1878	- - - **CELAENORRHININI** Swinhoe, 1912; **confirmed status**
- - - - - = **Tagiadini** Mabille, 1878	- - - **CARCHARODINI** Verity, 1940; **reinstated status**
- - - - - - ↕ *Thymelidae* Burmeister, 1878	- - - - - - ↕ *Erynnidi* Tutt, 1906
- - - - - - ↕ *Erynnidi* Tutt, 1906	- - - **ACHLYODIDINI** Burmeister, 1878; **new status**
- - - - - - ↕ *Nisoniadidi* Tutt, 1906	- - - **ERYNNINI** Brues & Carpenter, 1932; **confirmed status**
- - - - - - ↕ *Urbani* Durrant, 1919	- - - - - - ↕ *Thymelidae* Burmeister, 1878
- - - - - = **Erynninae** Brues & Carpenter, 1932	- - - - - - ↕ *Nisoniadidi* Tutt, 1906
- - - - - = **Carcharodidi** Verity, 1940	- - - **PYRGINI** Burmeister, 1878; **confirmed status**
- - - - - = **Coladeniina** Koçak & Seven, 1997	- - - - - = **Antigonini** Mabille, 1878
- - - - - = **Odontoptilina** Koçak & Seven, 1997	- - - - - - ↕ *Urbani* Durrant, 1919
- - **HETEROPTERINAE** Aurivillius, 1925	- - **HETEROPTERINAE** Aurivillius, 1925; **confirmed status**
- - - - - - ↕ *Eumesiidae* C. Felder & R. Felder, 1867	- - - - - - ↕ *Eumesiidae* C. Felder & R. Felder, 1867
- - - - - - ↕ *Cyclopidinae* Speyer, 1879	- - - - - - ↕ *Cyclopidinae* Speyer, 1879
- - - - - = **Carterocephalini** Orfila, 1949	- - - - - = **Carterocephalini** Orfila, 1949
- - **TRAPEZITINAE** Waterhouse & Lyell, 1914	- - **TRAPEZITINAE** Waterhouse & Lyell, 1914
- - - - - = **Hesperillidi** Voss, 1952	- - - - - = **Hesperillidi** Voss, 1952
- - **HESPERIINAE** Latreille, 1809	- - **HESPERIINAE** Latreille, 1809
- - - - - - ↕ *Pamphilinae* Butler, 1871	- - - - - - ↕ *Pamphilinae* Butler, 1871
- - - - - = **Carystini** Mabille, 1878	- - - **AEROMACHINI** Tutt, 1906; **new status**
- - - - - = **Erionotaria** Distant, 1886	- - - - - = **Ampittiini** Chou, 1994; **new status**
- - - - - = **Baorinae** Doherty, 1886	- - - - - = **Halpina** Koçak & Seven, 1997; **new status**
- - - - - = **Suastinae** Doherty, 1886	- - - ***INCERTAE SEDIS***
- - - - - = **Thymelicinae** Tutt, 1905	- - - - - = **Carystini** Mabille, 1878
- - - - - = **Aeromachinae** Tutt, 1906	- - - - - = **Erionotini** Distant, 1886
- - - - - = **Astictopterinae** Swinhoe, 1912	- - - - - = **Suastinae** Doherty, 1886
- - - - - = **Matapinae** Swinhoe, 1912	- - - - - = **Megathymini** J.H. Comstock & A.B. Comstock, 1895
- - - - - = **Notocryptinae** Swinhoe, 1912	- - - - - = **Astictopterinae** Swinhoe, 1912
- - - - - - ↕ *Erynninae* Swinhoe, 1913	- - - - - = **Matapinae** Swinhoe, 1912
- - - - - = **Plastinginae** Swinhoe, 1913	- - - - - = **Notocryptinae** Swinhoe, 1912
- - - - - - ↕ *Adopoeini* Clark, 1948 (emended)	- - - - - = **Plastinginae** Swinhoe, 1913
- - - - - = **Calpodini** Clark, 1948	- - - - - = **Calpodini** Clark, 1948
- - - - - = **Taractroceridi** Voss, 1952	- - - - - = **Aegialini** Stallings & Turner, 1958

Table 1
Continued

Previous suprageneric classification of the Hesperiidae*	Revised suprageneric classification of the Hesperiidae
- - - - - = **Ampittiini** Chou, 1994	- - - - - = **Agathymini** Stallings & Turner, 1959
- - - - - = **Ancistroidini** Chou, 1994	- - - - - = **Ancistroidini** Chou, 1994
- - - - - = **Gegenini** Chou, 1994	- - - - - = **Isoteinonini** Chou, 1994
- - - - - = **Isoteinonini** Chou, 1994	- - - - - = **Eogenina** Koçak & Seven, 1997
- - - - - = **Eogenina** Koçak & Seven, 1997	- - - - - = **Unkanina** Koçak & Seven, 1997
- - - - - = **Halpina** Koçak & Seven, 1997	- - - **TARACTROCERINI** Voss, 1952; **confirmed status**
- - - - - = **Itonina** Koçak & Seven, 1997	- - - **BAORINI** Doherty, 1886; **new status**
- - - - - = **Parnarini** Koçak & Seven, 1997	- - - - - = **Gegenini** Chou, 1994; **new status**
- - - - - = **Unkanina** Koçak & Seven, 1997	- - - - - = **Itonina** Koçak & Seven, 1997; **new status**
- - **MEGATHYMINAE** J.H. Comstock & A.B. Comstock, 1895	- - - - - = **Parnarini** Koçak & Seven, 1997; **new status**
	- - - **THYMELICINI** Tutt, 1905; **confirmed status**
- - - **MEGATHYMINI** J.H. Comstock & A.B. Comstock, 1895	- - - - - - ↕ *Adopoeini* Clark, 1948 (emended); **new status**
	- - - **MONCINI** A. Warren**, new tribe**
- - - **AEGIALINI** Stallings & Turner, 1958	- - - **HESPERIINI** Latreille, 1809; **confirmed status**
- - - **AGATHYMINI** Stallings & Turner, 1959	- - - - - - ↕ *Erynninae* Swinhoe, 1913

*This synonymy is based on the arrangement detailed in Appendix 1.

↕ = unavailable name. There are at least four family group names formed from the genus *Erynnis*, but only one of these is based on the genus properly identified. As dictated by Code articles 41 and 65.2.1 (ICZN, 1999), the case should be referred to the Commission for a ruling. In the meantime, we treat these names as if the Commission has ruled to suppress all but the one properly proposed name (Erynninae Brues and Carpenter, 1932).

HPLC-grade water (final elution volume between 50 and 500 μL, depending on amount of starting tissues), frozen at −20 °C, and corresponding wings and body parts (usually minus the thorax) stored in glassine envelopes. DNA and residual morphological materials will be permanently deposited in public institutions, as indicated in Appendix 2.

For each specimen, we amplified and sequenced a 943-bp fragment spanning the 3′ end of *COI*, the tRNAleu and the 5′ end of *COII*, 739 bp of *EF-1α* and 403 bp of the *wingless* gene (although in a few cases sequences for different genes were obtained from two specimens, as indicated in Appendix 2). Skipper-specific primers for *COI-COII* were developed (Gary and Susan, see Table 2), after obtaining preliminary sequences from primers listed in Brower and Jeansonne (2004) and Brower et al. (2006). Primers for *EF-1α* were taken from Cho et al. (1995) and Monteiro and Pierce (2001), and for *wingless* from Brower and DeSalle (1998); all primers used in this study are listed in Table 2. PCR amplifications were performed in a 50- or 100-μl reaction volume, on a Peltier thermal cycler (PTC-100, MJ Research, c/o Biorad, Hercules, CA, USA). Amplifications conducted in a 50-μL reaction volume included 3 μL of template, 5 μL of 10 × buffer (0.1 M Tris–HCl, 0.1 M KCl, 1% Triton X-100, pH 8.3), 5 μL of 25 μM $MgCl_2$, 1 μL of 10 μM dNTPs, 2 μL of each primer (10 μM), 0.3 μL *Taq* polymerase, and 31.7 μL distilled water. Amplifications conducted in a 100-μL reaction volume included 1 μL of template, 10 μL of 10 × buffer, 15 μL of 25 μM $MgCl_2$, 2 μL of 10 μM dNTPs, 2 μL of each primer (10 μM), 0.2 μL *Taq* polymerase, and 69 μL distilled water. The cycling profile for *COI-COII* and *wingless* was 4 min at 92 °C, and 40 cycles of 1 min at 94 °C, 0.5 or 1 min at

Table 2
Oligonucleotide primers used in this study

Name	Gene	Strand	Primer sequence	Position*
LepWG1	*wingless*	S	5′-GARTGYAARTGYCAYGGYATGTCTGG-3′	1111–1136
LepWG2	*wingless*	A	5′-ACTICGCRCACCARTGGAATGTRCA-3′	1750–1775
Rudy	*COI*	S	5′-GAAGTTTATATTTTAATTTTACCGGG-3′	2191–2217
Phyllis	*COI*	A	5′-GTAATAGCIGGTAAA/GATAGTTCA-3′	3275–3298
Gary	*COI*	S	5′-TAGGAATAATTTATGCMATAATAGC-3′	2276–2301
Susan	*COI*	A	5′-TTGTTGTTCTAATARAAATCG-3′	3242–3263
George I	*COI*	S	5′-ATACCTCGACGTTATTCAGA-3′	2772–2792
Eva	*COI*	A	5′-GAGACCATTACTTGCTTTCAGTCATCT-3′	3772–3799
Al	*EF-1α*	S	5′-GAGGAAATYAARAAGGAAG-3′	2582–2600
Tipper	*EF-1α*	A	5′-ACAGCVACKGTYTGYCTCATRTC-3′	3344–3367
Gennifer	*EF-1α*	A	5′-CGCACGGCAAAACGACCGAGRGG-3′	3320–3342

*Locations of the *wingless* primers in the *Drosophila melanogaster wingless* sequence (Rijsewijk et al., 1987); of the *COI-COII* primers in the *Drosophila yakuba* mitochondrial genome sequence (Clary and Wolstenholme, 1985), and the *Ef-1α* primers in the *Drosophila melanogaster* sequence as reported by Cho et al. (1995).

46 °C, and 2 min at 72 °C, and that for *EF-1α* was 2 min at 94 °C, and 32 cycles of 1 min at 94 °C, 1 min at 60 °C, and 1.5 min at 72 °C, followed by 10 min at 72 °C.

Amplified DNA fragments were cleaned with silica beads (Bio 101, Qbiogene, Irvine, CA, USA), or with Qiaquick PCR purification kits (Qiagen). Cleaned PCR products were cycle sequenced using ABI Prism or Big Dye kits (Applied Biosystems, Foster City, CA, USA), in a PTC-100, with the same primers as used for PCR. Recommended reaction conditions were used, along with the profile of 60 cycles of 0.5 min at 96 °C, 0.25 min at 50 °C, and 4 min at 60 °C. Single-stranded products were cleaned using ethanol and sodium acetate precipitation, and run on an ABI 373A or 377 automated sequencer or outsourced to Macrogen (Seoul, South Korea). All sequences were generated in both directions. Automated sequence outputs were edited manually and aligned by eye. Other than some minor length heterogeneity at the beginning and end of the tRNA and a single one-codon deletion in *wingless* (present in two taxa), there was no ambiguity in the alignment. Heterozygous positions in the nuclear genes (where simultaneous chromatogram peaks for two nucleotides appeared almost or exactly equal) were coded according to the IUPAC ambiguity codes. The aligned data matrix is available on the web at http://www.treebase.org. Individual sequences have been submitted to GenBank (accession codes given in Appendix 2).

Phylogenetic analysis

Data were concatenated and analysed as a single matrix under the parsimony criterion. Gaps were scored as missing; all characters and transformations were weighted equally. We searched for the most parsimonious cladograms from the unordered and equally weighted data matrix consisting of 215 taxa. Trees were rooted with *Papilio*, and other non-hesperiid taxa were included in the ingroup to test the monophyly of Hesperiidae. The parsimony analyses were performed in PAUP* 4.0b 10 (Swofford, 2002) using the parsimony ratchet (Nixon, 1999) as implemented in PAUP* by PAUPRat (Sikes and Lewis, 2001). The general ratchet analysis conditions were as follows: seed = 0, nreps = 200, wtmode = uniform. The percentage of characters perturbed during each iteration (pct) varied between 5, 10 and 15%. The search was repeated five times for each level of character perturbation, yielding a total of 15 independent ratchet searches. The maximum-parsiomiony (MP) tree length was corroborated in NONA 2.0 (Goloboff, 1999) using similar parameters as the PAUP* tree searches. In addition, we explored the structure of the data with separate analyses of each gene region, using heuristic searches with 1000 random addition replicates using tree bisection–reconnection (TBR) branch swapping with a single tree held during each step.

In the combined analysis, we evaluated character support and congruence among partitions for the clades in the strict consensus of the MP trees using branch support (BS: Bremer, 1988, 1994), partitioned branch support (PBS: Baker and DeSalle, 1997; Gatesy et al., 1999) and the partition congruence index (PCI: Brower, 2006b; see also Brower et al., 2006). Fractional PBS values were rounded to two decimal places. Due to the computationally intensive structure of the data set, BS values were calculated in PAUP* using PAUPRat-generated batch files that were modified to search anti-constraint trees generated from the MP tree set using TreeRot v.2. (Sorenson, 1999). Although tedious to set up by hand, the use of the parsimony ratchet to search for anti-constraint tree lengths consistently found shorter trees (resulting in lower BS values) than searches using standard PAUP* heuristic strategies. As in other recent studies (e.g. Wahlberg and Nylin, 2003; Wahlberg et al., 2003, 2005b), we refer to the support values as giving weak, moderate, good or strong support when discussing our results. We define 'weak support' as BS values between 1 and 2, 'moderate support' as BS values between 3 and 5, 'good support' as values between 6 and 10, and 'strong support' as values of 11 and greater. We endorse BS values over bootstrap values as they are a parameter of the data, rather than an estimate of tree stability based on pseudoreplicated subsamples of the data, and because they have no upper bound (Brower, 2006b).

Results and discussion

Characteristics of the data set

The total combined data consist of 2086 bp, 913 of which are invariant and 890 of which are parsimony-informative. Combining the three data sets in simultaneous parsimony analysis yields 90 trees of 19,123 steps (CI = 0.091, RI = 0.422), the strict consensus of which is shown in Figs 1 and 2. Up to 35 positions were coded as gaps in some taxa, including one gap in the *wingless* data set and three gaps in the *COI-COII* data set; all of these were easily detected when aligning by eye, as flanking regions were conserved. A few sequences are incomplete and 11 taxa are missing *wingless* sequences (see Appendix 2). Basic statistics for the three gene regions are shown in Tables 3 and 4.

In order to investigate incongruence (Mickevich and Farris, 1981; Farris et al., 1994), we conducted separate analyses of the three gene regions. Overall, the phylogenetic signal of *wingless* strongly conflicts with the other two gene regions (Table 3). Although *wingless*

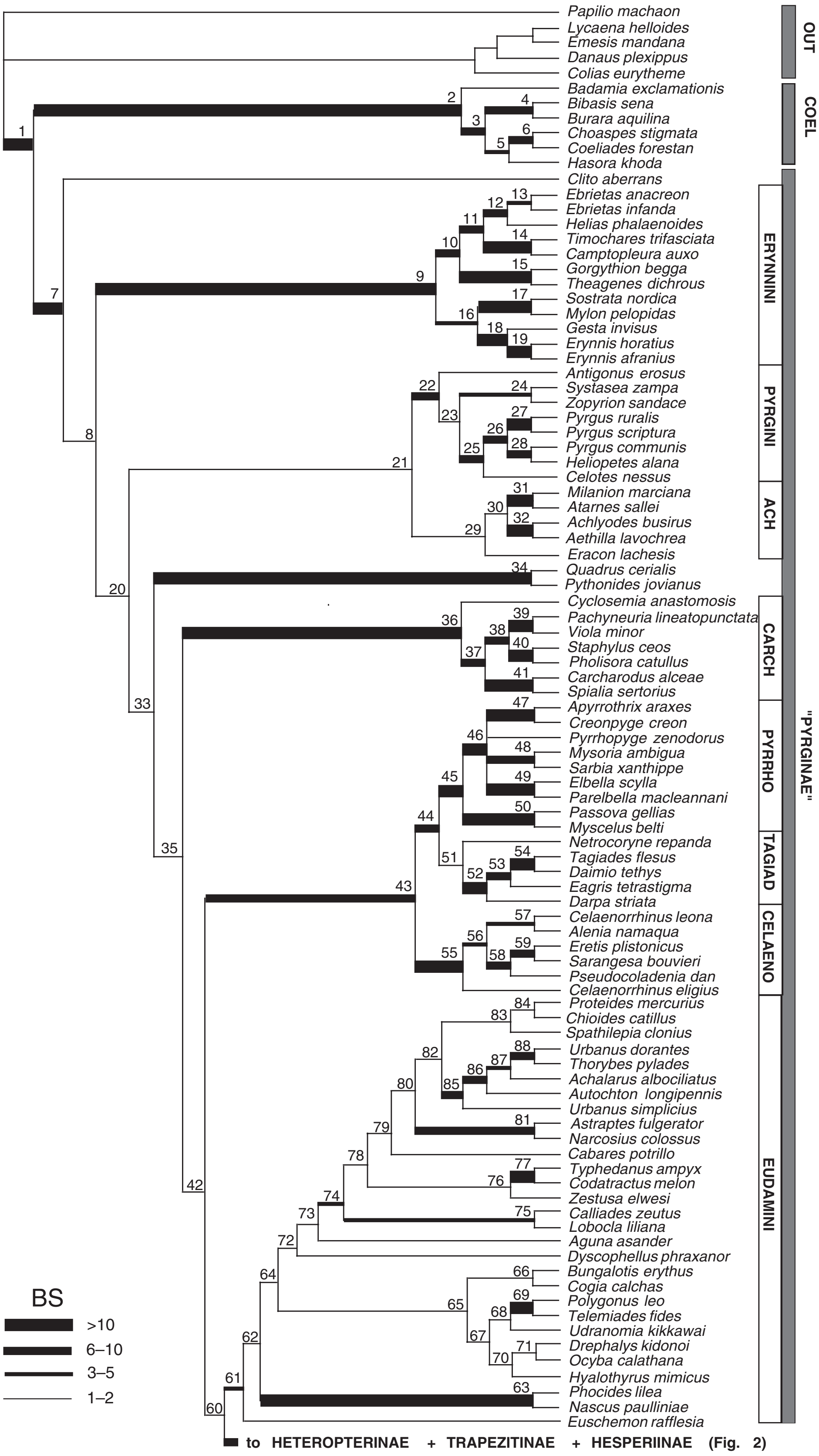
Papilio machaon
Lycaena helloides
Emesis mandana
Danaus plexippus
Colias eurytheme
Badamia exclamationis
Bibasis sena
Burara aquilina
Choaspes stigmata
Coeliades forestan
Hasora khoda
Clito aberrans
Ebrietas anacreon
Ebrietas infanda
Helias phalaenoides
Timochares trifasciata
Camptopleura auxo
Gorgythion begga
Theagenes dichrous
Sostrata nordica
Mylon pelopidas
Gesta invisus
Erynnis horatius
Erynnis afranius
Antigonus erosus
Systasea zampa
Zopyrion sandace
Pyrgus ruralis
Pyrgus scriptura
Pyrgus communis
Heliopetes alana
Celotes nessus
Milanion marciana
Atarnes sallei
Achlyodes busirus
Aethilla lavochrea
Eracon lachesis
Quadrus cerialis
Pythonides jovianus
Cyclosemia anastomosis
Pachyneuria lineatopunctata
Viola minor
Staphylus ceos
Pholisora catullus
Carcharodus alceae
Spialia sertorius
Apyrrothrix araxes
Creonpyge creon
Pyrrhopyge zenodorus
Mysoria ambigua
Sarbia xanthippe
Elbella scylla
Parelbella macleannani
Passova gellias
Myscelus belti
Netrocoryne repanda
Tagiades flesus
Daimio tethys
Eagris tetrastigma
Darpa striata
Celaenorrhinus leona
Alenia namaqua
Eretis plistonicus
Sarangesa bouvieri
Pseudocoladenia dan
Celaenorrhinus eligius
Proteides mercurius
Chioides catillus
Spathilepia clonius
Urbanus dorantes
Thorybes pylades
Achalarus albociliatus
Autochton longipennis
Urbanus simplicius
Astraptes fulgerator
Narcosius colossus
Cabares potrillo
Typhedanus ampyx
Codatractus melon
Zestusa elwesi
Calliades zeutus
Lobocla liliana
Aguna asander
Dyscophellus phraxanor
Bungalotis erythus
Cogia calchas
Polygonus leo
Telemiades fides
Udranomia kikkawai
Drephalys kidonoi
Ocyba calathana
Hyalothyrus mimicus
Phocides lilea
Nascus paulliniae
Euschemon rafflesia
OUT
COEL
ERYNNINI
PYRGINI
ACH
CARCH
PYRRHO
TAGIAD
CELAENO
EUDAMINI
"PYRGINAE"
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57 58 59 60 61 62 63 64 65 66 67 68 69 70 71 72 73 74 75 76 77 78 79 80 81 82 83 84 85 86 87 88
BS
>10
6–10
3–5
1–2
to HETEROPTERINAE + TRAPEZITINAE + HESPERIINAE (Fig. 2)

Fig. 1. Strict consensus of 90 most-parsimonious trees from the combined data set of all three genes. Length 19123 steps (CI = 0.091; RI = 0.422). Clade numbers are indicated above branches. Corresponding branch support values, partitioned branch support values and partition congruence indices are given in Table 4. Branch width relates to BS support values, as indicated in the legend in the lower left corner. Taxon names are listed in Appendix 2, together with voucher information. OUT = outgroup taxa, COEL = Coeliadinae, PYRRHO = Pyrrhopygini, TAGIAD = Tagiadini, CELAENO = Celaenorrhinini, ACH = Achlyodidini, CARCH = Carcharodini.

provides little positive BS support for any of the internal nodes (Table 4), the gene region may be informative at higher taxonomic levels: excluding *wingless* from the analyses resulted in a paraphyletic ingroup (results not shown). Of the 186 resolved ingroup branches, *COI-COII* provides positive support to 139 and contradicts 47, *EF-1α* supports 147 and contradicts 39, and *wingless* supports 51 and contradicts 135 (11 taxa are missing the *wingless* sequence). Seventeen branches are supported by all three gene regions, 103 supported only by *COI-COII* + *EF-1α*, 14 only by *COI-COII* + *wingless*, 18 only by *EF-1α* + *wingless*, 23 by *COI-COII* only, 25 by *EF-1α* only, and two by *wingless* only. Thus, although *COI-COII* and *EF-1α* appear to provide most of the phylogenetically informative characters, no single gene region drives the topology of the combined hypothesis of relationships, which is different from any of the trees implied by single genes analysed separately (results from separate analyses not shown).

The classification of Hesperiidae discussed below is based on the results of the combined cladistic analysis. The nomenclatorial philosophy we employ is that all named taxa should be monophyletic, and that taxa meeting this criterion should bear names and ranks associated with them in the historical literature to the greatest degree possible. BS values for individual clades are indicated below (also see Table 4). In the text below, numbers in parentheses after the names of taxa refer to the numbered clades in Figs 1 and 2.

Subfamily-level relationships

This is the first comprehensive phylogenetic analysis of relationships within the family Hesperiidae. Previous phylogenetic studies of the family have been limited by insufficient taxon sampling, either lacking sufficient taxa for adequate resolution (e.g. de Jong et al., 1996; Warren, 2004), or including taxa sampled on a regional basis only (Chiba et al., 2001), and therefore lacking major sections of diversity present in the family. Other family-level studies of the Hesperiidae have not employed a cladistic methodology, and/or have scored and analysed characters in an ambiguous way (Voss, 1952; Scott, 1985; Scott and Wright, 1990; Atkins, 2005). In our study, we have identified several clades that are strongly supported by three gene regions, as well as clades that are less robust and likely to change with the addition of more characters.

Our data imply that the family Hesperiidae (1), as currently circumscribed, is monophyletic with strong support (BS 13), in agreement with the results of Wahlberg et al. (2005a). Six of seven currently recognized subfamilies of Hesperiidae are recovered as monophyletic clades (although not all represent subfamily-level taxa, see Figs 1 and 2), with the following relationships: (Coeliadinae + (“Pyrginae” including Pyrrhopyginae + (Heteropterinae + (Trapezitinae + Hesperiinae including Megathyminae)))). Monophyly of Coeliadinae (2) receives strong support (BS 12), and its basal position sister to the rest of the Hesperiidae corroborates the results of de Jong et al. (1996) and Wahlberg et al. (2005a). Although Pyrrhopyginae (45) is monophyletic, with strong support (BS 23), it is placed deep within one of the clades comprising “Pyrginae” (7), where its sister relationship to a clade (51) containing members of Evans’ Tagiades group receives good support (44: BS 7). Pyrginae of previous authors is a paraphyletic grade of five major and two minor clades (Figs 1 and 2), including Pyrrhopyginae and *Euschemon*; these clades are discussed in detail below. Monophyly of Heteropterinae (89: minus *Tsitana*, see below) receives strong support (BS 14), and its position as sister to Trapezitinae (95) + Hesperiinae (108) receives good support (93: BS 9). Trapezitinae (95) is monophyletic with strong support (BS 19), and its position as sister to Hesperiinae corroborates the results of Wahlberg et al. (2005a, but Heteropterinae was not included). Monophyly of Hesperiinae (108) receives moderate support (BS 5). The two genera included in our analysis from Megathyminae (or “giant skippers”) are sister taxa with strong support (129: BS 43), but this clade is placed deep within Hesperiinae, in a polytomy (110) with various Asian and African genera, also including the Neotropical genera *Orses*, *Perichares* (Carystus group) and *Pyrrhopygopsis* (Calpodes group). Additional taxa and characters will be needed to elucidate the phylogenetic position of the giant skippers.

In summary, our results imply that four subfamilies of Hesperiidae should be recognized: Coeliadinae, Heteropterinae, Trapezitinae and Hesperiinae. “Pyrginae” is a paraphyletic grade of seven clades, some of which should be recognized as tribal-level taxa. Further study is needed before a satisfactory classification of the “Pyrginae” will be possible, and additional characters and/or taxa are needed to elucidate the phylogenetic positions of *Euschemon rafflesia* and the giant skippers.

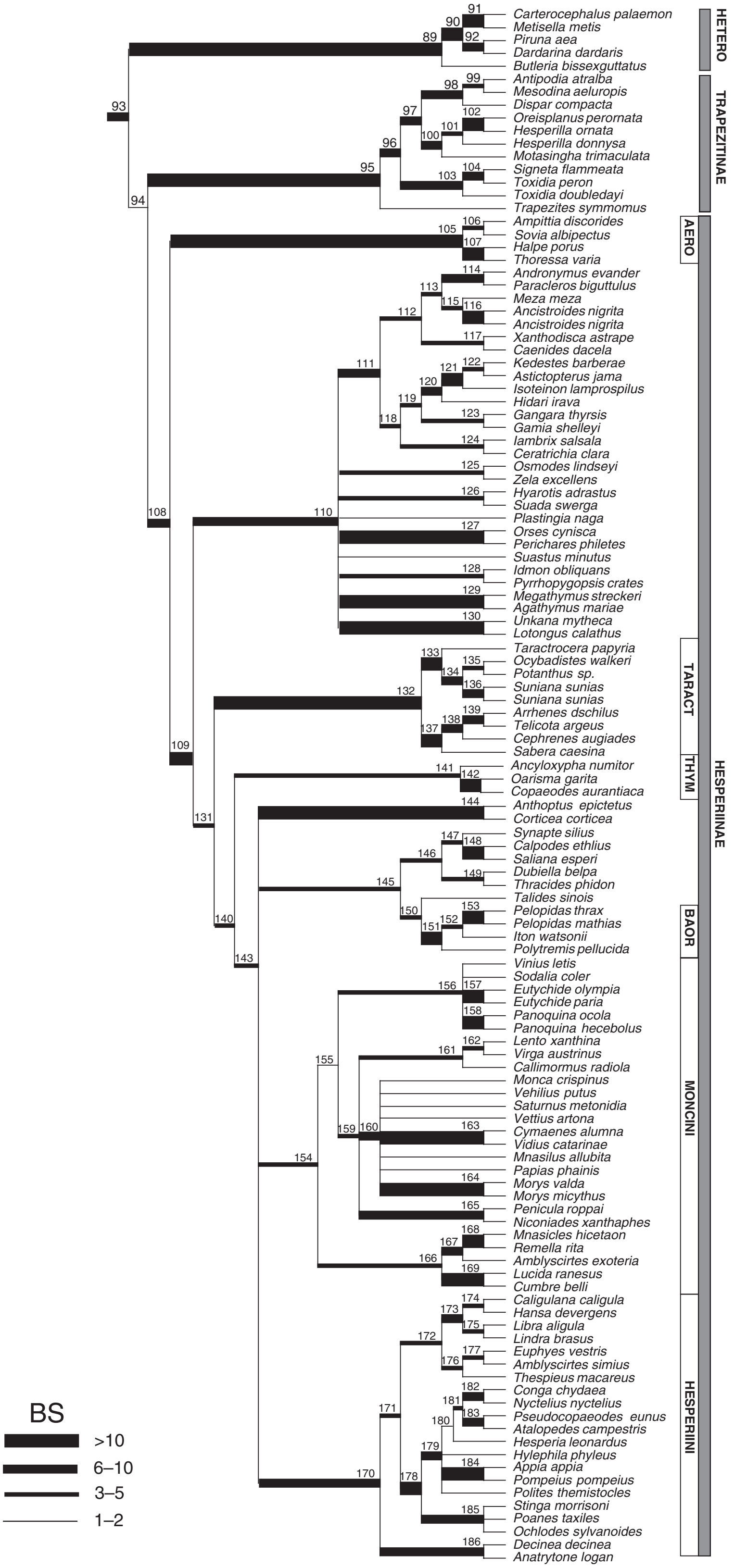

Fig. 2. Continuation of the cladogram shown in Fig. 1. HETERO = Heteropterinae, AERO = Aeromachini, BAOR = Baorini, THYM = Thymelicini, TARACT = Taractrocerini.

Table 3
Parameter estimates of the data for individual gene regions and the entire matrix

Gene region	# Bases	Informative sites	Min. steps	# Trees	Shortest tree	Intrinsic homoplasy	D homoplasy	Total support
COI	943	427	976	16442	9725	8749 (90.0%)		1004.3
Ef-1a	740	259	566	11308	4581	4013 (87.6%)		1637.1
*Wingless**	403	204	478	> 60000	4285	3807 (88.8%)		844.45
Combined	2086	890	2020	90	19123	17103 (89.4%)	532 (2.78%)	1796.95

*Eleven taxa missing *wingless* sequences were deleted from this analysis.

Monophyly of Evans' generic groups and subgroups

As shown in Table 5, only five of Evans' 28 generic groups within the various subfamilies of Hesperiidae were recovered as monophyletic clades, although we did not sample enough genera to assess the monophyly of the Isoteinon group or two groups of Pyrrhopyginae (Oxynetrini and the monotypic Zoniini). One of the monophyletic groups is Heteropterinae (89, equivalent to Evans' Carterocephalus group), which has since been widely regarded as a subfamily-level taxon (see Warren, 2006). Two of Evans' monophyletic genus-groups are in Pyrrhopyginae (46, 50), and were subsequently modified and elevated to tribal-level taxa by Mielke (2001). The other two monophyletic genus-groups are both within Hesperiinae: the Taractrocera group (132), which is strongly supported (BS 12; eight of 13 genera included), and the Gegenes group (151), which is also strongly supported (BS 30; three of 14 genera included) but is situated within a clade of hesperiines from several other groups (145, as discussed below). The remaining 23 generic groups defined by Evans are para- or polyphyletic, according to our results.

Only three of Evans' 38 generic subgroups were recovered as monophyletic clades (see Table 5), although we did not sample enough taxa to assess the monophyly of eight of these (excluding monotypic subgroups). The monophyletic groups are the Tagiades subgroup of the Tagiades group (54: BS 28; strongly supported but only two of ten genera included, which were once considered congeneric), the Paramimus subgroup of the Telemiades group (31: BS 55; very strongly supported, two of five genera included), and the Thymelicus subgroup of the Hesperia group (141: BS 4; moderate support, three of five genera included). The remaining subgroups are para- or polyphyletic. Based on these results, the use of Evans' generic groups and subgroups as a basis for a tribal classification cannot be considered satisfactory.

Paraphyly of Pyrginae

As noted above (Figs 1 and 2), our data suggest that Pyrginae of previous authors (e.g. Evans, 1937, 1949, 1952, 1953) is a paraphyletic grade composed of several clades. This result is not surprising, as several recent workers have questioned the monophyly of the group. In the morphological analyses conducted by de Jong et al. (1996; see also Ackery et al., 1999), Pyrginae was "never" recovered as a monophyletic group, although their study included just ten skipper taxa. Larsen (2005) went as far as to say that "Pyrginae is certainly not monophyletic". In the combined molecular (three genes) and total evidence (molecular plus morphological) analyses conducted by Wahlberg et al. (2005a), only two species of pyrgines were included (*Pyrgus* and *Urbanus*), but these never formed a monophyletic group. Our data also failed to recover Pyrginae as a monophyletic group, although relationships implied (Fig. 1) among the clades of "Pyrginae" (8, 20, 33, 35, 42: all BS 1) receive weak support with strong incongruence among data partitions, and the arrangement of these clades is not likely to be robust to the addition of more characters. However, two (9, 36) of the five "major" clades in this group are strongly supported, and appear to represent tribal-level taxa, while components of the remaining major clades (21, 43, 61) are also strongly supported and appear to represent tribal-level taxa, as discussed below. Until the clades of "Pyrginae" can be studied in more detail through the addition of more characters (e.g. morphology), and relationships between them can be better understood, we retain "Pyrginae" as an informal subfamily-level grouping composed of various tribes, but acknowledge its paraphyly by placing the name in quotation marks.

The sister taxon to other "Pyrginae" + Heteropterinae + Trapezetinae + Hesperiinae with weak support (8: BS 1) is the aptly named *Clito aberrans*. Throughout the course of this study, the position of *C. aberrans* has varied with the inclusion of additional taxa; various data sets have implied relationships with *Quadrus* + *Pythonides*, *Milanion* + *Atarnes*, and *Eracon*, among others. Evans (1953) placed *Clito* in his Antigonus subgroup of the Telemiades group, a placement retained by subsequent workers (e.g. Cock, 1998; Austin, 2000), none of whom has questioned its genus-group placement or commented on unusual morphological features. Based on this, we consider the current basal position of *Clito* in Fig. 1 to be spurious, and do not believe it represents its actual relationship to other members of "Pyrginae" (trees just two steps longer place *Clito* between *Quadrus* + *Pythonides* and *Milanion* + *Atarnes*). Of the six

Table 4
Support indices for the branches in Figs 1 and 2. Partitioned branch support

Clade number	COI	wg	Ef-1α	Branch support	Partition congruence index
1	−10.7	16.97	6.73	13	11.35
2	3.47	−12.12	20.65	12	9.98
3	−19.04	11.97	14.07	7	1.56
4	4.47	−10.03	14.56	9	6.77
5	10.36	−9.2	2.84	4	−0.6
6	14.32	−15.55	10.23	9	5.54
7	20.93	−7.78	−0.15	13	11.78
8	0.24	−8.76	9.52	1	−16.52
9	2.97	4.97	10.07	18	18
10	0.3	3.8	1.9	6	6
11	6.63	−1.87	5.24	10	9.63
12	1.3	−5.37	14.07	10	8.93
13	6.13	−7.87	5.74	4	0.06
14	−3.82	−0.65	17.46	13	12.3
15	0.63	−0.22	13.6	14	13.98
16	0.24	−8.76	9.52	1	−16.52
17	3.97	2.35	9.68	16	16
18	30.81	−15.19	1.38	17	15.21
19	3.5	−8.1	17.6	13	11.75
20	0.24	−8.76	9.52	1	−16.52
21	0.24	−8.76	9.52	1	−16.52
22	0.47	1.13	5.4	7	7
23	0.24	−8.76	9.52	1	−16.52
24	6.13	2.63	−4.76	4	1.62
25	19.78	−13.04	−0.74	6	1.41
26	0.75	−9.77	16.02	7	4.21
27	11.23	3.81	3.96	19	19
28	−17.14	12.51	14.63	10	6.57
29	0.24	−8.76	9.52	1	−16.52
30	0.24	−8.76	9.52	1	−16.52
31	25.45	18.32	11.22	55	55
32	10.42	11.31	2.27	24	24
33	0.24	−8.76	9.52	1	−16.52
34	14.72	2.3	3.98	21	21
35	0.24	−8.76	9.52	1	−16.52
36	3.56	13.87	−3.42	14	13.52
37	4.21	6.23	−2.44	8	7.39
38	−2.64	14.6	−2.96	9	7.76
39	0.23	11.57	28.2	40	40
40	5.61	1.09	18.3	25	25
41	0.76	−5.16	16.4	12	11.14
42	0.24	−8.76	9.52	1	−16.52
43	−7.93	4.73	10.2	7	4.73
44	30.88	−21.87	−2.01	7	0.18
45	18.05	−11.53	16.48	23	22
46	12.13	−1.17	13.03	24	23.89
47	17.63	−2.37	−3.23	12	11.1
48	4.52	−7.48	11.96	9	7.34
49	19.32	−14.85	9.53	14	11.88
50	−5.37	13.3	26.07	34	33.68
51	2.8	−3.37	2.57	2	−1.37
52	−7.87	−5.37	24.23	11	8.58
53	15.13	−5.7	−3.43	6	2.96
54	11.8	6.66	9.54	28	28
55	0.14	15.95	−3.09	13	12.52
56	11.3	−5.2	−3.1	3	−2.53
57	8.9	0.83	−4.73	5	3.11
58	−8.83	−1.27	19.1	9	6.76
59	−15.65	1.53	24.12	10	6.87
60	0.24	−8.76	9.52	1	−16.52
61	21.59	−14.95	−1.64	5	−1.64
62	0.24	−8.76	9.52	1	−16.52
63	6.31	−6.15	17.84	18	17.32
64	0.24	−8.76	9.52	1	−16.52
65	0.24	−8.76	9.52	1	−16.52
66	9.8	−9.03	0.23	1	−17.06
67	0.24	−8.76	9.52	1	−16.52
68	0.24	−8.76	9.52	1	−16.52
69	1.99	5.26	13.75	21	21
70	0.24	−8.76	9.52	1	−16.52
71	0.24	−8.76	9.52	1	−16.52
72	0.24	−8.76	9.52	1	−16.52
73	−7.56	1.49	13.07	7	4.84
74	25.21	−14.79	−5.42	5	−3.08
75	18.06	−12.89	−0.17	5	−0.22
76	0.24	−8.76	9.52	1	−16.52
77	60.25	−30.35	−2.91	27	24.53
78	0.24	−8.76	9.52	1	−16.52
79	0.24	−8.76	9.52	1	−16.52
80	0.24	−8.76	9.52	1	−16.52
81	26.79	−14.86	−4.93	7	1.53
82	0.24	−8.76	9.52	1	−16.52
83	0.24	−8.76	9.52	1	−16.52
84	1.4	−9.43	9.03	1	−17.86
85	7.86	−6	6.14	8	6.5
86	21.74	−12.41	−1.33	8	4.57
87	14.58	−11.12	−0.46	3	−4.72
88	29.04	−18.44	−3.6	7	0.7
89	−10.19	10.23	13.96	14	12.54
90	−5.53	7.13	11.4	13	12.15
91	4.63	3.43	5.93	14	14
92	12.8	−4.03	−0.77	8	6.8
93	−7.51	6.84	9.67	9	7.33
94	19.58	−11.95	−5.63	2	−15.58
95	5.87	0.2	12.93	19	19
96	1.53	−13.35	19.82	8	4.66
97	−3.7	1.35	9.35	7	5.94
98	15.4	−7.93	0.53	8	6.02
99	1.17	−0.9	2.73	3	2.4
100	−25.01	9.1	24.91	9	3.44
101	10.49	−7.52	2.03	5	1.99
102	−2.2	−0.8	22	19	18.68
103	−11.87	−3.37	24.24	9	5.61
104	0.8	−6.87	12.07	6	3.71
105	10.74	8.49	−7.23	12	10.8
106	3.97	0.63	−1.6	3	1.93
107	23.25	2.5	−0.74	25	24.95
108	8.3	−3.03	−0.27	5	3.68
109	−9.94	−3.92	27.86	14	12.02
110	14.16	−14.86	6.7	6	1.05
111	1.44	−7.92	13.48	7	4.74
112	18.05	−15.37	1.32	4	−3.69
113	−9.62	−7.43	22.05	5	−1.82
114	−0.03	−14.37	23.4	9	5.80
115	−3.67	−2.79	11.46	5	2.42
116	50.15	−3.42	34.28	81	80.93
117	7.47	−7.03	3.56	4	0.48
118	14.28	−15.57	5.29	4	−3.79
119	−3.79	−8.68	16.47	4	−2.24
120	−5.37	2.63	10.74	8	6.66
121	6.55	−1.1	9.55	15	14.85

Table 4
Continued

Clade number	COI	wg	Ef-1α	Branch support	Partition congruence index
122	−11.75	−1.6	17.35	4	−2.68
123	7.57	−12.01	9.44	5	0.2
124	−11.89	−1.72	17.62	4	−2.81
125	−2.45	−4.87	11.32	4	0.34
126	2.15	−6.45	8.3	4	0.78
127	10.8	3.78	12.43	27	27
128	12.76	−11.2	2.44	4	−1.6
129	9.13	−3.58	37.42	43	42.8
130	1.62	−4.71	15.09	12	11.22
131	4.24	0.13	−1.37	3	2.09
132	15.25	−1.87	−2.38	11	10.23
133	−0.21	9.68	8.53	18	17.98
134	−5.78	−2.4	15.18	7	4.66
135	2.24	−10.24	13	5	0.9
136	−1.57	−8.44	17.01	7	4.14
137	16.76	−14.99	10.23	12	9.5
138	−0.93	−6.07	14	7	5
139	1.83	−1.6	5.77	6	5.47
140	2.97	2.17	−2.14	3	1.57
141	−2.18	2.21	3.97	4	2.91
142	−5.53	9.37	10.16	14	13.21
143	−3.6	−2.43	11.03	5	2.59
144	16.99	−11.40	12.41	18	16.73
145	−6.57	−6.9	16.47	3	−5.98
146	1.07	−10.43	14.36	5	0.83
147	1.39	−13.28	16.89	5	−0.31
148	7.55	1.26	5.19	14	14
149	−2.57	−3.9	11.47	5	2.41
150	2.6	−11.3	13.7	5	0.48
151	10.95	−7.24	20.3	24	23.41
152	15.8	−15.7	3.9	4	−3.85
153	−6.2	9.8	13.4	17	16.27
154	−0.16	−3.7	8.86	5	3.46
155	2.94	3.65	−4.59	2	−2.59
156	0.8	−0.87	4.07	4	3.57
157	14.99	0.13	9.88	25	25
158	29.63	−8.2	13.57	35	34.53
159	2.73	−8.27	10.54	5	1.69
160	10.15	−8.68	8.53	10	8.26
161	13.13	−12.37	4.24	5	0.05
162	27.7	−13.61	−5.09	9	4.84
163	16.68	5.44	−1.12	21	20.89
164	15.43	−9.47	10.04	16	14.82
165	−6.38	5.06	7.32	6	3.87
166	3.65	−9.6	10.95	5	1.16
167	−10.27	−2.12	20.39	8	4.9
168	−5.39	−4.81	21.2	11	9.15
169	7.73	−11.27	18.53	15	13.49
170	−3.12	−5.14	16.26	8	5.94
171	2.16	−6.82	9.66	5	2.27
172	−0.86	−5.71	10.57	4	0.72
173	6.73	−11.1	12.37	8	5.23
174	15.97	4.55	−16.52	4	−4.26
175	22.95	−17.72	−1.23	4	−5.48
176	6.15	−7.77	6.62	5	1.89
177	−11.6	−2.93	19.53	5	−0.81
178	15.9	−17.1	12.2	11	7.89
179	20.89	−8.34	−6.55	6	1.04
180	−1.67	2.67	0	1	−2.34
181	25.97	−16.2	−4.77	5	−3.39
182	33.63	−15.2	−8.43	10	5.27
183	24.9	−18.01	1.11	8	3.5
184	7.47	10.3	−0.77	17	16.91
185	−1.23	−5.39	14.62	8	6.35
186	0.3	−3.37	13.07	10	9.33

remaining clades of the paraphyletic "Pyrginae", two of them are strongly supported (9: BS 18; 36: BS 14; corresponding to Erynnini and Carcharodini, see below), as is the small clade including just *Quadrus* and *Pythonides* (34: BS 21). Strongly supported components of the remaining three clades of "Pyrginae" include clade 45 (BS 24), corresponding to the Pyrrhopyginae of previous authors, and clade 55 (BS 13), which mostly includes members from Evans (1937, 1949) Celaenorrhinus group.

This is the first study to challenge the subfamily-level status of Pyrrhopyginae (Mielke, 2005; but see Wahlberg et al., 2005a); however its phylogenetic position deeply nested within "Pyrginae" (clade 45) has been robust to the addition of taxa and characters over the course of this study (e.g. Warren, 2004). When "Pyrginae" has appeared as a paraphyletic grade, as in the current study, Pyrrhopyginae never formed one of its "major" subdivisions. Given the topology of our cladogram, maintenance of the Pyrrhopyginae as a subfamily-level taxon would require recognition of at least seven additional subfamilies (clades 9, 22, 29, 36, 51, 55, 61) within what is currently circumscribed as "Pyrginae". In discussing the secondary sexual characters that partly serve to delineate groups within Pyrginae, Ackery et al. (1999) noted, "At first sight there is no apparent reason why the Pyrrhopyginae could not be a subordinate taxon of Pyrginae". Our results support that hypothesis.

In trees just two steps longer than the most parsimonious tree set, Pyrginae is recovered as a weakly supported monophyletic group, composed of two major clades. One of these clades includes members of clades 9, 21, 34, 36 and 43 (Fig. 1), while the other major clade includes the same taxa as clade 61 (BS 5), including members of Evans' Augiades and Urbanus groups, also including a few species from the Celaenorrhinus and Telemiades groups (see below), as well as *Euschemon rafflesia*. The position of *E. rafflesia* at the base of this clade (62) is weakly supported (BS 1, with strong incongruence among partitions), and in trees just a few steps longer, *E. rafflesia* falls out of this clade into an unresolved polytomy including the rest of the Pyrginae. Thus, it would not be surprising if the phylogenetic position of *E. rafflesia* changes with the addition of

Table 5
Monophyly of Evans' subfamilies and generic groups (as modified by Ackery et al., 1999 and Mielke, 2001), based on taxa sampled for this study.

Group or subgroup	Monophyletic?
Hesperiidae	Yes
Coeliadinae	Yes
Pyrrhopyginae	Yes (but within "Pyrginae")
Pyrrhopygini	Yes
Zoniini	Monotypic
Passovini	Yes
Oxynetrini	?
Pyrginae	No
Augiades group	No
Urbanus group	No
Celaenorrhinus group	No
"Old World" subgroup	No
Bungalotis subgroup	No
Nascus subgroup	Monotypic
Porphyrogenes subgroup	?
Celaenorrhinus subgroup	No
Tagiades group	No
Netrocoryne subgroup	No
Tagiades subgroup	Yes
Caprona subgroup	?
Telemiades group	No
Telemiades subgroup	No
Nisoniades subgroup	No
Staphylus subgroup	No
Quadrus subgroup	No
Pythonides subgroup	No
Paramimus subgroup	Yes
Antigonus subgroup	No
Erynnis group	No
Pyrgus group	No
Heteropterinae	Yes (*Tsitana* excluded)
Trapezitinae	Yes
Hesperiinae	Yes (including Megathyminae)
Astictopterus group	No
Astictopterus Subgroup	?
Ampittia Subgroup	No
Halpe Subgroup	No
Isoteinon group	?
Ceratrichia group	No
Acleros group	No
Ploetzia group	No
Ancistroides group	No
Plastingia group	No
Plastingia subgroup	No
Erionota subgroup	No
Unkana subgroup	No
Prada subgroup	?
Vinius group	No
Apaustus group	No
Apaustus subgroup	No
Phanes subgroup	?
Cymaenes subgroup	No
Lerema subgroup	No
Vettius subgroup	?
Carystus group	No
Phlebodes group	No
Phlebodes subgroup	No
Oeonus subgroup	No
Hesperia group	No
Thymelicus subgroup	Yes
Hesperia subgroup	No
Phemiades subgroup	No
Lerodea group	No
Calpodes group	No
Calpodes subgroup	No
Niconiades subgroup	No
Aides subgroup	?
Thracides subgroup	No
Chloeria subgroup	Monotypic
Pseudosarbia subgroup	?
Taractrocera group	Yes
Gegenes group	Yes
Megathyminae	Yes (but within Hesperiinae)

further data. However, our results highlight the affinity of *Euschemon* with other Hesperiidae, and suggest that the species belongs in this family, despite its morphological peculiarities.

Circumscription of tribes

No tribal-level classification has been proposed for Coeliadinae (2) or Heteropterinae (89), both of which are 'small' subfamilies with fewer than 15 genera. Morphology of the coeliadine genera is rather uniform (Ackery et al., 1999), and it seems unlikely the subfamily will be further subdivided in the future. Morphology of Heteropterinae is also rather uniform (Ackery et al., 1999), although its circumscription remains incomplete. Evans (1937) placed the genera *Tsitana* and *Lepella* in his African Astictopterus group (part of his Hesperiinae), together with *Metisella* and *Hovala*. Bridges (1993) retained all of these genera in the Astictopterus group, but Larsen (2005) included them all in Heteropterinae. When *Tsitana* is included in our combined analysis (data not shown), it groups with members of Evans' African Astictopterus and Ampittia groups (such as *Astictopterus*, *Isoteinon* and *Kedestes*, clade 121), well within Hesperiinae. We were unable to sample *Hovala*, but Evans (1937) believed it to be closely related to *Metisella*, and in our tree *Metisella* is sister to *Carterocephalus* (a genus undoubtedly related to *Heteropterus*), with strong support (91: BS 14). We were also unable to sample *Lepella*, and some other putative heteropterine genera, as indicated in Appendix 1. Therefore, we make no attempt to subdivide the Heteropterinae further, although further subdivision may be warranted with the addition of more taxa and characters.

Voss (1952) divided Trapezitinae (95) into two tribes, "Trapezitidi" (explicitly including just *Trapezites*) and "Hesperillidi". He divided the latter into two unnamed groups based on the presence or absence of a stigma on the male forewing, and on the number of metatibial spurs. One group (with a stigma and two pairs of spurs) explicitly included *Dispar*, *Hesperilla*, *Signeta*, and *Toxidia*, while the other group (without a stigma and with one pair of spurs) explicitly included only *Mesodina*. However, Waterhouse (1932) and various subsequent authors have recognized three major groupings within the Trapezitinae (e.g. Atkins, 1973; Common and Waterhouse, 1981; Ackery et al., 1999) that do not directly overlap with Voss' tribes, based on differences in larval foodplant families and characters of the larvae and pupae. These include (1) 'trapezitine' genera feeding primarily on Xanthorrhoeaceae and Poaceae (*Trapezites*, *Anisynta*, *Pasma*, *Neohesperilla*, *Dispar*, *Toxidia*, *Signeta*, and *Croitana*), (2) 'hesperilline' genera feeding only on Cyperaceae (*Oreisplanus*, *Hesperilla*, and *Motasingha*), and (3) the 'mesodine' genus feeding on Iridaceae (*Mesodina*). Larval foodplants of the New Guinean genera *Hewitsoniella* and *Felicena* remain unknown (Parsons, 1999), and foodplants of the genus *Rachelia* have recently been found to be in the Flagellariaceae (Braby, 2004). Recent research on relationships of trapezetine genera (e.g. Atkins, 1973, 1984, 1994) has not supported Waterhouse's groupings, and a separate informal grouping, the 'Proeidosa group,' has been proposed for *Croitana* and two recently described genera, *Proeidosa* and *Antipodia* (see Atkins, 1984, 1994). Despite the informal groupings identified by various authors, no formal tribal-level classification for the subfamily Trapezitinae has been employed since Voss' study (e.g. Bridges, 1993; Atkins and Edwards, 1996; Braby, 2000, 2004). Our results do not support the monophyly of Voss' tribes, but do support the monophyly of Waterhouse's three 'hesperilline' genera (100: BS 9). Our results also indicate that the 'trapezitine' genera are polyphyletic. When three other 'trapezitine' genera are added to our combined analysis (*Anisynta*, *Neohesperilla* and *Pasma*), for which data from only two genes is currently available, this arrangement does not change (data not shown). More genera are required to test the monophyly of the Proeidosa group, and its relationship to *Mesodina*. Until additional genera can be sampled and additional characters can be included (including those from immature stages), we feel it is premature to propose a tribal-level classification for the Trapezitinae.

The Megathyminae (or "giant skippers", clade 129) have previously been divided into three tribes (Stallings and Turner, 1958, 1959), an arrangement which has persisted among some authors (e.g. Mielke, 2004, 2005). However, many authors have treated the giant skippers as a family-level taxon within Hesperioidea (e.g. Comstock and Comstock, 1895; Barnes and McDunnough, 1912; Lindsey, 1921; Lindsey et al., 1931; McDunnough, 1938; Brown et al., 1956; dos Passos, 1964; Freeman, 1969b; Roever, 1975; Bridges, 1993). Our results indicate that the giant skippers are apparently a highly derived group of hesperiines (see Table 1), corroborating the views of Scott and Wright (1990) and Ackery et al. (1999). Furthermore, our results fail to support even tribal-level status for giant skippers, although such a status should not be ruled out until morphological characters are also considered.

As we have included only 35% of the world's genera of Hesperiidae in our combined analysis, inclusion of all skipper genera into a tribal classification must await a comprehensive morphological study to put our results into a broader context (A. Warren, J.R. Ogawa and A.V.Z. Brower, unpublished data). However, we have been able to identify certain clades with good or strong support, which are likely to be robust to the addition of taxa and characters, and appear to represent tribal-level entities. Recent efforts to construct a tribal nomenclature for Pyrginae and Hesperiinae have been regional in nature and are largely based on Evans' regional generic groups (Chou, 1994, 1998; Koçak and Seven, 1997). Based on our results (Figs 1 and 2), we propose a cosmopolitan tribal classification for "Pyrginae" and Hesperiinae, using available family-level names, to complement our revised subfamily-level arrangement (see Table 1). As the tribes of "Pyrginae" are arranged in a weakly supported paraphyletic grade (Fig. 1), the order in which they are discussed below does not imply any particular relationship among tribes, and mostly follows the order presented by Evans (1937, 1949, 1952, 1953).

Tribes of "Pyrginae"

Eudamini, ***confirmed status*** *(61)*. This clade includes members of Evans' Augiades and Urbanus groups, as well as some members of his Celaenorrhinus and Telemiades groups (see Appendix 1). Recently, Mielke (2004, 2005) has arranged genera in Evans' Augiades and Urbanus groups, and American representatives of the Celaenorrhinus group, under the tribe Eudamini. Mielke's Eudamini (62: BS 1) was recovered as a weakly supported monophyletic group, with the addition of *Spathilepia*, *Cogia* and *Telemiades* (from the Telemiades group), and the removal of *Celaenorrhinus*. The Asian genus *Lobocla* (75, from the Celaenorrhinus group) is also included in Eudamini. As discussed above, *Euschemon rafflesia* is situated at the base of this clade, in a sister relationship with Mielke's Eudamini. For now we include *Euschemon* within Eudamini, although it is stressed that this placement should be considered tentative, until morphological characters can also be evaluated together with our molecular data. For the most part, relationships within the Eudamini are poorly supported by our data, although the monophyly of the clade including *Urbanus* (which itself is paraphyletic, see below), *Thorybes*, *Achalarus*, and *Autochton* receives good support (85: BS 8), and the sister relationships between *Phocides* + *Nascus* (63: BS 18), *Polygonus* + *Telemiades* (69: BS 21), and *Typhedanus* + *Codatractus*

(77: BS 27) are strongly supported. Eudamini was originally proposed by Mabille (1877), and has been used at the tribal level by various authors (e.g. Mabille, 1878; Tutt, 1906 – in Tutt 1905–1914; Clark, 1948; Mielke and Casagrande, 1998; Lamas, 2003; Mielke, 2004, 2005).

*Pyrrhopygini, **reinstated status** (45)*. Evans' (1951) generic groups for Pyrrhopyginae were modified and given tribal-level status by Mielke (2001). We were unable to sample representatives of two of these tribes, Oxynetrini and Zoniini (which is monotypic), but the monophyly of the two tribes we were able to sample, Pyrrhopygini (46: BS 24) and Passovini (50: BS 34), is strongly supported by our data. Inclusion of three additional genera for which we currently have only partial data (*Yanguna*, *Jemadia* and *Mimoniades*; data not shown) does not change the circumscription of Mielke's tribes. However, due to the position of Pyrrhopyginae within "Pyrginae" (Fig. 1), we treat the former subfamily as a tribe of "Pyrginae". This action changes the status of the tribes described by Mielke (2001), which can now be known as sub-tribes: Pyrrhopygina (46, **new status**), Zoniina (**new status**), Passovina (50, **new status**) and Oxynetrina (**new status**). Pyrrhopygini was originally proposed by Mabille (1877), and was emended to Pyrrhopyginae by Watson (1893), a spelling employed by all subsequent authors who recognized the group as a subfamily-level taxon (Mielke, 2005).

*Tagiadini, **confirmed status** (51)*. Monophyly of Tagiadini receives weak support (BS 2) from our data, although the sister relationship (44: BS 7) between the New World Pyrrhopygini (45) and the Old World Tagiadini (51) receives good support. Relationships within Tagiadini receive good (53: BS 6) and strong support (52: BS 11; 54: BS 28). Not all members of Evans' Tagiades group are included within Tagiadini as defined by our cladogram (Fig. 1), which has the following topology: (*Netrocoryne* + (*Darpa* + (*Eagris* + (*Daimio* + *Tagiades*)))). We have incomplete data (two genes) for two additional genera, *Gerosis* and *Odontoptilum*, that when included in the combined analyses (data not shown) are also situated in this clade. Members of this tribe largely include those placed in the Tagiadini by Chou (1994, 1998), with the exception of *Sarangesa* and *Pseudocoladenia* (see below). Tagiadini was first proposed by Mabille (1878).

*Celaenorrhinini, **confirmed status** (55)*. This clade (BS 13) is sister to Tagiadini + Pyrrhopygini, with good support (43: BS 7). According to our data, Evans' Celaenorrhinus group, given tribal status by Chou (1994, 1998), is polyphyletic. As noted above, *Lobocla* is in the Eudamini, and *Euschemon* is also tentatively placed there. In addition, all members sampled from Evans' New World subgroups of the Celaenorrhinus group (including *Bungalotis*, *Dyscophellus*, *Nascus*, and *Ocyba*) are situated within Eudamini (63, 66, 71, 72). However, *Celaenorrhinus* species, along with a few additional genera, do form a monophyletic clade with strong support (BS 13), which appears to represent a tribal entity (Fig. 1). Genera in our study included within Celaenorrhinini are *Celaenorrhinus*, *Pseudocoladenia*, *Sarangesa*, *Eretis*, and *Alenia*. *Eretis* was formerly placed in Evans' Tagiades group, while *Alenia* was placed in Evans' Pyrgus group, based on similarities in wing pattern and antennal nudum number to the other 'checkered skippers', such as *Pyrgus* and *Spialia*. Relationships within Celaenorrhinini receive moderate (56: BS 3; 57: BS 5) and good (58: BS 9; 59: BS 10) support. The name "Celaenorrhinae" was first proposed by Swinhoe (1912), and was emended to Celaenorrhinini by Clark (1948), who treated the group as a tribe of the Pyrginae, in which he included species from Evans' Telemiades, Erynnis, and Pyrgus groups.

*Carcharodini, **reinstated status** (36)*. This clade is strongly supported (BS 14) by our data, and is composed of members of Evans' Telemiades (*Pachyneuria*, *Viola*, *Cyclosemia*, *Staphylus*) and Pyrgus (*Spialia*, *Carcharodus*, *Pholisora*) groups, with the following topology: (*Cyclosemia* + (*Carcharodus* + *Spialia*) + ((*Pachyneuria* + *Viola*) + (*Staphylus* + *Pholisora*))). Members of this clade occur widely in the Palaearctic (*Carcharodus*), African (*Spialia*), and Neotropical regions (remaining genera), extending to the Nearctic (*Pholisora*). Relationships within the Carcharodini receive good (37: BS 8; 38: BS 9) and strong support (40: BS 25; 41: BS 12), including the sister relationship between *Staphylus* and *Pholisora* (39: BS 40), corroborating Lindsey's (1921; also see Lindsey et al., 1931 and Stanford, 1981) belief that these genera are closely related (*contra* Evans, 1953). The name "Carcharodidi" was first proposed by Verity (1940), was used as a tribal name by Picard (1947), and was treated as a subtribe by Koçak (1989).

*Achlyodidini, **new status** (29)*. The union of *Achlyodes* + *Aethilla* (both from Evans' Erynnis group) is strongly supported by our data (32: BS 24), although the clade uniting these genera with *Milanion* + *Atarnes* (30: BS 1) is weakly supported, as is the union of *Eracon* (from Evans' Telemiades group) with the other four genera (29: BS 1). Although *Achlyodes* and *Aethilla* are fairly similar skippers on morphological grounds (e.g. Warren, 1996), we see few characters that might suggest a close relationship between them, *Atarnes* + *Milanion*, and *Eracon*, and suggest that the clade (29) may not be robust to the addition of characters and taxa in future studies. However, the union of *Atarnes* + *Milanion* with *Achlyodes* + *Aethilla* has appeared in many analyses of these data over the course of this study, even though usually with weak support. In addition, *Quadrus* and *Pythoniades*, herein represented on their own clade within "Pyrginae" (Fig. 1), have often grouped with *Atarnes* + *Milanion* in previous analyses. We therefore suspect that the position of *Quadrus* + *Pythoniades* is likely to change in future analyses employing additional characters and/or taxa. The name "Achlyodidae" was proposed by Burmeister (1878) and has not since been used at the family level.

*Erynnini, **confirmed status** (9).* This clade is strongly supported (BS 18) by our data, and has been surprisingly robust to the addition of taxa and characters over the course of this study. Erynnini is composed of most members of Evans' Erynnis group, excluding *Achlyodes* and *Aethilla* (see above), and including some members of Evans' Telemiades group (*Gorgythion*, *Sostrata*, *Mylon*). Relationships within Erynnini mostly receive good (10: BS 6; 11: BS 10; 12: BS 10) and strong support (14: BS 13; 15: BS 14; 17: BS 16; 18: BS 17; 19: BS 13). Recently, Chou (1994, 1998) resurrected use of the name Erynnini at the tribal level for the sole Chinese representative of this clade, *Erynnis*. There is some question as to the correct authorship of the name Erynnini. At least four family-group names have been formed from the genus *Erynnis* (see Table 1), but only one of these, Erynnini Brues and Carpenter, 1932; is based on the genus as properly identified. As dictated by Code article 65.2.1 (ICZN, 1999), the case should be referred to the Commission for a ruling on each of these names. In the meantime, we treat these names as if the Commission has ruled to suppress all but the one properly proposed name (Table 1). Mielke (2005) credited Barnes and Lindsey (1922) with the authorship of "Erynninae". However, Barnes and Lindsey merely mentioned Erynninae as a possible replacement name for the subfamily Hesperiinae (known in recent decades as Pyrginae), and explicitly chose "Urbaninae" as their replacement name. Thus, it is unclear if Erynninae Barnes and Lindsey, 1922, can be considered to be validly proposed (ICZN, 1999 art. 12). If so, it has precedence over Brues and Carpenter's (1932) authorship.

*Pyrgini, **confirmed status** (22).* Whereas Chou (1994, 1998) applied the name Pyrgini to Chinese members of Evans' Pyrgus group, Mielke (2004, 2005) recently applied Pyrgini in a much broader way, to all New World genera of Pyrginae that were not included in Eudamini (*sensu* Mielke, 2004). As currently composed, with good support (22: BS 7), Pyrgini (Fig. 1) includes members of Evans' Pyrgus and Telemiades groups. Relationships within Pyrgini receive weak (23: BS 1), moderate (24: BS 4), good (25: BS 6; 26: BS 7; 28: BS 10), and strong support (27: BS 19). *Xenophanes*, for which we currently have only partial data (two genes), is also situated in this clade when it is included in our combined analyses (data not shown). One noteworthy aspect of our results is that the genera of 'checkered skippers' (*Pyrgus*, *Spialia*, *Alenia*), placed by Evans in his Pyrgus group, are undoubtedly polyphyletic, and are placed in three separate tribes (Pyrgini, Carcharodini and Celaenorrhinini, respectively).

Tribes of Hesperiinae

*Aeromachini, **new status** (105).* This clade is strongly supported (BS 12) by our data, and is sister to the rest of the Hesperiinae. Aeromachini includes some (but not all) members of Evans' Astictopterus group, including all three members of Evans' Halpe subgroup that were included in our analysis (*Halpe*, *Thoressa*, *Sovia*). The sister relationship between *Halpe* and *Thoressa* is strongly supported (107: BS 25), although our data provide only moderate support for the sister relationship between *Ampittia* and *Sovia* (106: BS 3). Although we were unable to sample the genus *Aeromachus* (the type genus of Aeromachini), its close relationship to *Ampittia*, *Halpe*, *Thoressa*, and *Sovia* is supported by the great similarity of male genital structures across these genera (as discussed and figured by Evans, 1937, 1949, and Inoué and Kawazoé, 1966), and we do not hesitate to associate *Aeromachus* at the tribal level with the four genera we studied. Aeromachini is apparently equivalent to the "Halpe group" proposed by Inoué and Kawazoé (1966), probably excluding *Arnetta* (see Eliot, 1978). Tutt (1906) originally proposed "Aeromachinae" as a subfamily and "Aeromachidi" as a tribe for Aeromachus, *Ampittia*, and *Taractrocera*, although *Taractrocera* belongs in a different tribe (see below).

Clade 110. This clade receives good support from our data (BS 6), but we consider its present composition to be tentative, as it contains a disparate mix of taxa that we feel are unlikely to be monophyletic, based on their morphology. In addition, the composition of this clade has varied widely over the course of this study (data not shown), and the large polytomy at clade 110 demonstrates the unresolved nature of relationships among taxa currently placed here. This clade mostly includes Old World genera from Evans' Astictopterus, Isoteinon, Ceratrichia, Acleros, Ploetzia, Ancistroides, and Plastingia groups, but also includes New World genera from Evans' Carystus and Calpodes groups, and Megathyminae (giant skippers). Despite the presence of a few strongly supported relationships (e.g. 121: BS 15), we feel that the composition of this clade is likely to change with the addition of more taxa and characters, and that its subdivision into more than one tribe in the future seems likely. However, the addition of *Koruthaialos*, *Notocrypta*, *Pemara*, *Pyroneura*, *Gretna*, and *Pterotei-*

non in alternative analyses, for which we had only partial data (two genes), does not change the overall composition of this clade (data not shown).

As discussed above, the placement of giant skippers in this clade is not supported by any obvious morphological or biological evidence, but does suggest that they are 'highly derived' hesperiines that do not represent a family- or subfamily-level taxon. Although we are confident that the giant skippers are a derived hesperiine clade, we stress that additional study is required to determine their phylogenetic position within the Hesperiinae.

The tropical American genera *Perichares* and *Orses* were included in Evans' Carystus group. Their sister relationship is strongly supported (127: BS 27) by our data, but their relationship to other taxa in this clade is unresolved. Like the giant skippers, their placement in this clade has been robust to the addition of taxa over time, although their position within the clade has varied (data not shown). The placement of *Pyrrhopygopsis* (from Evans' Calpodes group) in this clade has been less stable (e.g. Warren, 2004).

Although the current composition of this clade is highly heterogenous, most of the Old World genera (at least) are likely to be closely related to each other, with respect to other tribes in the subfamily. Should clade 110 or groups therein prove to be robust to the addition of characters and taxa in future studies, several family-group names are available for members of this clade (Table 1), and we have sampled type genera of many of these (Appenedix 2). However, none of these names has been widely used in the literature (see Mielke, 2005). Because of the heterogeneous nature of this grouping, we apply no family-group name to Clade 110 at this time, until its monophyly can be corroborated in future studies; the tentative placement of all associated family-group names is *incertae sedis* (Table 1).

Taractrocerini, ***confirmed status*** *(132).* Voss (1952) was the first to treat this group as a tribal entity within Hesperiinae, but his concept of the group also included members of Thymelicini (from Evans' Thymelicus subgroup). Recently, Chou (1994, 1998) employed the tribe Taractrocerini for Chinese members of Evans' Taractrocera group. de Jong (1990, 2001, 2003) studied relationships of 13 genera in this group, *sensu* Evans (1949, minus *Prusiana*), and noted that the group is apparently monophyletic. One of the few genus groups proposed by Evans that formed a monophyletic group in our study, the clade comprising Taractrocerini (132) is strongly supported by our data (BS 11), and is sister to the remaining tribes of the Hesperiinae, discussed below. Relationships between genera of Taractrocerini, as indicated by our data, do not entirely agree with those proposed by de Jong (2001, 2003), suggesting that more taxa need to be sampled in order to better resolve relationships in this tribe. For the most part, relationships among genera in this clade receive moderate or good support from our data, although two primary clades are strongly supported (133: BS 18; 137: BS 12).

Thymelicini, ***confirmed status*** *(141).* Tutt (1905, in Tutt 1905–1914) proposed the subfamily "Thymelicinae" and tribe "Thymelicidi" for members of the genus *Thymelicus* (an arrangement followed by Tutt, 1906; and 1906 in Tutt 1905–1914), but Evans (1949) included *Thymelicus* in his Hesperia group, an action followed by Voss (1952), who placed the genus in his tribe "Hesperiidi". Subsequently, Evans (1955) created the Thymelicus subgroup of his Hesperia group, in which he included *Thymelicus*, *Adopaeoides*, *Ancyloxypha*, *Oarisma*, and *Copaeodes* (see Appendix 1), the last three genera included by Voss in his tribe "Taractroceridi". Recently, Chou (1994, 1998) employed the name Thymelicini at the tribal level, in which he included just *Thymelicus*, the sole Chinese representative of this group. Although *Thymelicus* was not included in our study, as noted by Evans (1949, 1955), *Thymelicus* species share morphological features of the antennae, palpi, and male genitalia with the other four genera in his Thymelicus subgroup. de Jong (1984) and de Prins et al. (1992) figured the female genitalia of several *Thymelicus* species. Häuser (1993) commented on the peculiar structure of the corpus bursae in female *Thymelicus*, with a sclerotized ductus bursae interrupted by a membranous region where the ductus seminalis originates, and suggested this condition may represent a synapomorphy for the Thymelicus subgroup. Examination of the female genitalia of *Ancyloxypha*, *Oarisma* and *Copaeodes* (A.D.W. pers. obs.) has shown that the structure of the ductus bursae in these three species is similar to that found in *Thymelicus*, adding further evidence of a close relationship between them. Based on these morphological similarities, we apply the name Thymelicini to our clade (141) containing *Ancyloxypha*, *Oarisma*, and *Copaeodes*. However, monophyly of this clade receives only moderate support (BS 4) by our data, and the addition of *Thymelicus* and *Adopaeoides* in future studies is needed to test the stability of Thymelicini. Nevertheless, the sister relationship between *Oarisma* and *Copaeodes*, as implied by our data, is strongly supported (142: BS 14).

Baorini, ***new status*** *(151).* As noted above, our data strongly support the monophyly of Evans' Old World Gegenes group (151: BS 24), although only three genera from the group were included in our final analysis. We were unable to sample *Baoris*, but it shares many pupal and genitalic characters with *Pelopidas*, *Polytremis*, and *Iton*, as shown by Evans (1937, 1949) and especially by Bascombe et al. (1999), and we do not hesitate to associate *Baoris* with our three sampled genera, at the tribal level. The genus *Caltoris*, for which we currently have only partial data (two genes), is also situated in Baorini (151) when included in alternative analyses (data not shown). "Baorinae" was proposed by Doherty (1886), and was subsequently used at the subfamily level by Bell (1920, 1921, 1926), who included *Baoris*, *Caltoris*, *Chapra* (a junior subjective synonym of *Pelopidas*), *Parnara*, *Gegenes*, and *Iton* in the group (all of which were subsequently placed in Evans' 1949 Gegenes group, and in Chou's 1994, 1998 Gegenini).

However, our final analysis placed *Talides*, a New World genus from Evans' Carystus group, as sister to Baorini, with moderate support (150: BS 5). In addition, a moderately supported clade (146: BS 5) including members of Evans' Vinius (*Synapte*), Carystus (*Dubiella*) and Calpodes (*Calpodes*, *Saliana*, *Thracides*) groups is sister to the clade including *Talides* + Baorini, with moderate support (145: BS 3). While *Dubiella*, *Calpodes*, *Saliana*, and *Thracides* share various morphological characters (e.g. Evans, 1955), the inclusion of *Synapte* in this clade defies any obvious explanation, as it is a much smaller skipper and is morphologically more similar to some other genera in the Vinius group. These genera (excluding *Synapte* but possibly including *Talides*), along with related taxa (various genera from the Carystus and Calpodes groups), may eventually warrant tribal status, but for now we do not associate any family-group name with this clade (146). Should these genera occupy a tribal-level position in future studies, two names are potentially applicable, Carystini Mabille, 1878; and Calpodini Clark, 1948 (see Table 1).

Clade 144. A strongly supported clade (144: BS 18), including the New World genera *Anthoptus* and *Corticea* (from Evans' Vinius group), is part of a polytomy including Baorini and associated clades, and the following two tribes (Fig. 2). The position of this clade basal to the following two tribes, or in a polytomy with them, has been consistent over the course of this study, as characters and taxa have been added (data not shown). Although it is possible that this clade represents a tribal-level entity, we feel that the addition of more characters or taxa is needed to corroborate our results, and for now do not associate any family-group name with this clade. We also note that no family-group name is currently available for this clade (Table 1).

*Moncini A. Warren, **new tribe** (154)*. Type Genus: *Monca* Evans, 1955; – This clade receives moderate support (154: BS 5), and includes genera from Evans' Vinius (*Lento*, *Vinius*), Apaustus (*Callimormus*, *Virga*, *Mnasicles*, *Sodalia*, *Lucida*, *Vidius*, *Monca*, *Cymaenes*, *Vehilius*, *Mnasilus*, *Remella*, *Papias*, *Morys*, *Cumbre*, *Vettius*, *Eutychide*), Phlebodes (*Saturnus*, *Penicula*), Lerodea (*Amblyscirtes exoteria* – see below) and Calpodes (*Panoquina*, *Niconiades*) groups. Additional genera, for which we have incomplete data (two of three genes), are situated in this tribe in alternative analyses (data not shown), including *Lerodea* (from the Lerodea group), *Parphorus* (from the Apaustus group), *Mucia* (from the Phlebodes group), and *Halotus* (from the Calpodes group). We note that *Halotus* is sister to *Niconiades*, as predicted by Burns (1992a) based on morphological similarities. Although many relationships among genera in the Moncini receive good or strong support, the large polytomy at clade 160 probably reflects the need to sample additional taxa. We were surprised to find that, despite the abundance of family-group names that have been proposed for Old World groups of Hesperiinae, no name is available to apply to clade 154.

Morphology of genera in this clade is rather diverse, and despite molecular characters that differentiate (ICZN 1999 Art. 13.1.1) Moncini from other tribes in our analysis, no putative morphological synapomorphies have yet been identified to diagnose the tribe. However, all genera we include in Moncini have forewing vein M2 originating much nearer to M3 than M1, and most species are "little brown skippers" (although some have yellow, tawny, or other colourful markings). Adults of some genera (e.g. *Callimormus*, *Virga*) have a long, slender, pointed third segment of the labial palpi (like that found in Thymelicini and some Taractrocerini). Secondary sexual characters of males include the variable presence of forewing stigmata, and in some genera (e.g. *Vinius*), a tuft of hair-like scales on the dorsal hindwing.

*Hesperiini, **confirmed status** (170)*. Clark (1948) first recognized the tribe Hesperiini, in which he included various members of Evans' Apaustus, Hesperia, and Lerodea groups. Voss (1952) recognized the tribe "Hesperiidi", which included some members of Evans' Taractrocera, Hesperia, and Lerodea groups. Recently, Chou (1994, 1998) employed the name Hesperiini at the tribal level to represent *Hesperia* and *Ochlodes*, the sole Chinese genera in this group. In our study, this clade (170) is composed of members of Evans' Phlebodes, Hesperia, Lerodea, and Calpodes groups, and receives good support from our data (BS 8). Other than genera now placed in Thymelicini (141, see above), all genera in Evans' Hesperia group appear to be members of Hesperiini (except *Halotus*, see above). Some genera from Evans' Oeonus subgroup of the Phlebodes group are situated in this clade (*Decinea*, *Caligulana*, *Conga*), as are some members of Evans' Calpodes group (*Thespieus*, *Nyctelius*, *Lindra*) and one species from Evans' Lerodea group (*Notamblyscirtes simius*—see below). In addition, *Xeniades* (from Evans' Calpodes group), for which we currently have only partial data, is situated in this clade when included in our analyses, as sister to *Thespieus* (data not shown). For the most part, relationships between genera of Hesperiini receive moderate or good support by our data. Two clades receive strong support, including 178 (BS 11), and *Appia* + *Pompeius* (184: BS 17).

Genus-level relationships

More than one species from certain genera were included in our analysis. In both cases where two individuals of the same species were included, they emerged as sister taxa (116 *Ancistroides nigrita*, 136 *Suniana sunias*). However, in cases where two or more species from a genus were included, some congeners emerged as sister taxa (13 *Ebrietas infanda* + *E. anacreon*; 19 *Erynnis afranius* + *E. horatius*; 27 *Pyrgus scriptura* + *P. ruralis*; 153 *Pelopidas mathias* + *P. thrax*; 157 *Euytchide olympia* + *E. paria*; 158 *Panoquina ocola* + *P. hecebolus*; 164 *Morys micythus* + *M. valda*), while congeners discussed below did not.

We sampled two species of *Urbanus* (*sensu* Evans, 1952), *U. dorantes* and *U. simplicius*, members of Eudamini ("Pyrginae"). These did not emerge as sister taxa in our analysis, supporting Steinhauser's (1987) conclusion that the genus *Urbanus* is polyphyletic. *Urbanus dorantes* emerged in a sister relationship with *Thorybes pylades* (88: BS 7), and *U. simplicius* is sister to (*Autochton* + (*Achalarus* + (*U. dorantes* + *T. pylades*))), with good support (85: BS 8).

As noted by various authors (e.g. Lindsey and Miller, 1965; de Jong, 1982; de Jong and Treadaway, 1993; Austin and Steinhauser, 1996; Larsen, 2005), the pyrgine genus *Celaenorrhinus* is the only pan-tropical skipper genus. As discussed by de Jong (1982), this genus displays considerable morphological diversity, both in wing pattern and in the distribution of secondary sexual characters. We sampled one New World (*C. eligius*) and one Old World (*C. leona*) species of *Celaenorrhinus*, which did not appear as sister taxa in our analysis. *Celaenorrhinus eligius* emerged as sister to the remaining genera of Celaenorrhinini (55: BS 13), but *C. leona* is sister to *Alenia*, with moderate support (57: BS 5). Despite this, as we sampled just two of over 90 currently recognized species of *Celaenorrhinus* (Vane-Wright and de Jong, 2003), we feel it is premature to challenge the monophyly of the genus, as defined by de Jong (1982).

As currently circumscribed, the genus *Pyrgus* has an unusual Holarctic and Neotropical distribution (Warren, 1926; de Jong, 1972). We sampled three New World species of *Pyrgus*: *P. ruralis*, *P. scriptura* and *P. communis*. Two of these, *P. ruralis* and *P. scriptura*, emerged as sister taxa, with strong support (27: BS 18), while *P. communis* emerged as sister to *Heliopetes*, with good support (28: BS 7). This suggests that the genus *Pyrgus* may be paraphyletic with respect to *Heliopetes* and *Heliopyrgus* (see Austin and Warren, 2001). Until additional species of *Pyrgus*, *Heliopyrgus*, and *Heliopetes* can be sampled, we retain *P. communis* and its New World relatives (e.g. *P. c. chloe*, *P. albescens*, *P. adepta*, *P. orcynoides*, *P. oileus*, *P. orcus*, *P. brenda*, *P. philetas*, *P. veturius*; see Austin and Warren, 2001) in the genus *Pyrgus*, but stress that this arrangement requires further study, and note that a new genus is perhaps needed at least for the primarily Neotropical *P. communis* group.

Within Trapezitinae, we sampled two species of *Toxidia* and two species of *Hesperilla*, but neither genus emerged as a monophyletic clade. *Toxidia peron* emerged as sister to *Signeta flammeata* (104: BS 6), and *Toxidia doubledayi* emerged as sister to *T. peron* + *S. flammeata* (103: BS 9). As noted by Atkins et al. (1991) based on the morphology of immatures and adults, *Signeta* is very closely related to *Toxidia*, and the two genera are separated primarily on the basis of differences in the size and shape of the male forewing stigma. Our results suggest that *Toxidia* may be paraphyletic with respect to *Signeta*, but we feel that the other species of *Signeta* (*S. tymbophora*), and additional species of *Toxidia* should be sampled and analysed before formally changing the composition or synonymy of these genera. The genus *Hesperilla* is morphologically diverse, with multiple species groups (Atkins, 1978). The two *Hesperilla* species we sampled are *H. ornata* and *H. donnysa*. *Hesperilla ornata* emerged as sister to *Oreisplanus pernornata*, with strong support (102: BS 19), while *H. donnysa* is sister to *H. ornata* + *O. perornata* (101: BS 5). These results suggest that *Hesperilla* may be paraphyletic with respect to *Oreisplanus*, and that *Oreisplanus* might best be considered a 'species group' of *Hesperilla*. However, until the remaining species of *Oreisplanus* (*O. munionga*) and the 12 remaining species of *Hesperilla* can be sampled, we hesitate to disrupt the current generic arrangements (e.g. Atkins and Edwards, 1996; Braby, 2000, 2004).

Burns (1990) commented on the hesperiine genus *Amblyscirtes*, placed by Evans (1955) in his Lerodea group. He suggested that *Amblyscirtes* is not related to other members of the Lerodea group, and that it was closely related to genera in Evans' Apaustus group, such as *Mnasicles* and *Remella*. He also noted that one species, *simius*, did not belong in *Amblyscirtes*, based on male genitalia that "differ radically" from other species in the genus. However, over concern that *simius* may be related to a Neotropical genus unfamiliar to him, Burns treated *simius* as *incertae sedis*, and did not suggest to which of Evans' groups of hesperiine genera it may belong. Scott (2006) subsequently proposed the generic name *Notamblyscirtes* for *simius*. In addition to *N. simius*, we sampled one *Amblyscirtes* species, *A. exoteria*, whose presence in *Amblyscirtes* has not been disputed (e.g. Burns, 1990). According to our results, the two species are situated in separate tribes. *Notamblyscirtes simius* is in Hesperiini, in a sister relationship with *Euphyes* (177: BS 5). *Amblyscirtes exoteria*, presumably along with other *Amblyscirtes* species, is situated in Moncini, in a sister relationship with *Mnasicles* + *Remella* (167: BS 8), corroborating Burns' (1990) conclusion.

Conclusion

Here we have proposed a new family-level synonymy for the Hesperiidae, and have made a preliminary effort to establish a tribal nomenclature for the family (Table 1). We have identified several strongly supported monophyletic taxa, such as Pyrrhopygini, Erynnini, Trapezitinae, Aeromachini, and Taractrocerini, and have demonstrated strong support for the monophyly of the family. We have defined several unresolved issues that require further study, such as the paraphyly of "Pyrginae" and the phylogenetic position of "Megathyminae", a group we tentatively consider to be infra-tribal. We feel that the addition of more taxa and characters will be required to strengthen hypotheses of relationships presented here, but that our current arrangement represents a more natural classification than that proposed by Evans and modified by subsequent authors. We plan a second publication that will combine these data with morphological characters, and will use comparative morphology to integrate all genera of the Hesperiidae into a tribal classification (A. Warren, J.R. Ogawa and A.V.Z. Brower, unpublished data).

Acknowledgements

We offer sincere thanks to all those who provided specimens, without whom this study would not have been possible: Andrew Atkins, Jim Brock, Ernst Brockmann, Hide Chiba, Alexey Devyatkin, Scott Fitzgerald, Alan Heath, Yu-Feng Hsu, Daniel Janzen, Darlene Judd, Akito Kawahara, David Lohman, Kazuma Matsumoto, A. L. Monastyrskii, Debra Murray, Paul Opler, Tom Ortenburger, Michael Overton, Naomi Pierce, H. Tsukiyama, John Shuey, Jon D. Turner, Niklas Wahlberg, and Michael Whiting. We are grateful to our Brazilian colleagues for their ongoing support of our efforts. Thanks to Gi-Ho Sung for help operating the sequencing machine. Thanks also to former members of the Judd-Brower laboratory (Oregon State University) for help and support with various aspects of this research: Jessica Adkins, Scott Fitzgerald, Miranda Jeansonne, Jason Leathers, Ming-Min Lee, Kelsey Miller, Debra Murray, Karina Silva-Brandão, Kim Tanner, Jill Townzen, and Alaine Whinnett. We also thank Andrew Atkins, Bernard Hermier, Rienk de Jong, Torben Larsen, Paul Opler, Jonathan Pelham and Niklas Wahlberg for comments on early versions of this manuscript, and George Austin, Michael Braby, Hideyuki Chiba, Alexey Devyatkin, Harold Greeney, Yu-Feng Hsu, Daniel Janzen, Darlene Judd, David Lees, Christopher Marshall, Olaf Mielke, Paul Severns, Alvin Smith, and Joey Spatafora for discussions. This research was supported by the Harold and Leona Rice Endowment for Systematic Entomology, NSF DEB 0089886 and DEB 0640301 to A.V.Z.B., and NSF Doctoral Dissertation Improvement Grant DEB-039005 to A.V.Z.B. and A.D.W. Additional funding was provided to A.D.W. by Howard and Edna Mae Warren, and by the McGuire Center for Lepidoptera and Biodiversity and DGAPA-UNAM during the final phase of this study.

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Appendix 1

Hesperiidae genera of the world

The arrangement of the Coeliadinae follows Evans (1937, 1949), Tsukiyama (1985), Maruyama (1991), Ackery et al. (1995), Chiba (1995, 1997) and Vane-Wright and de Jong (2003); the arrangement of the Pyrrhopyginae follows Evans (1951) and Mielke (1995, 2001, 2002, 2004, 2005); the arrangement of the Pyrginae follows Evans (1937, 1949, 1952, 1953), Shirôzu and Saigusa (1962), Freeman (1969a), Mielke (1977, 2004, 2005), de Jong (1982), Steinhauser (1986, 1989), Ackery et al. (1995), Burns (1996, 1999), Warren (1996, 2000), Austin (1997), Austin and Warren (2001), Burns and Janzen (2005) and Larsen (2005); the status and arrangement of the Heteropterinae follows Higgins (1976), Warren (2000, 2001a,b), Mielke (2004, 2005), and Larsen (2005); the arrangement of the Trapezitinae follows Atkins (1973, 1984, 1994), Mayo and Atkins (1992), Atkins and Edwards (1996), Parsons (1999), and Braby (2000, 2004); the arrangement of the Hesperiinae follows Evans (1937, 1949, 1955), Lindsey and Miller (1965), Miller (1965), Mielke (1968, 1980, 1992), Steinhauser (1974, 1991), Eliot (1978- in part), de Jong (1983), Maruyama (1991), Burns (1992a,b, 1994a,b), Bridges (1993), de Jong and Treadaway (1993), Chiba and Tsukiyama (1994), Ackery et al. (1995), Devyatkin (1996, 2002), Austin (1997), Austin and DeVries (2001), Mielke and Casagrande (2002, 2003), Vane-Wright and de Jong (2003), Larsen (2005), Scott (2006), and Fan et al. (2007); the status and arrangement of the Megathyminae follows Freeman (1969b) and Mielke (2004, 2005), but see Ackery et al. (1999) and Opler and Warren (2002).

Genera represented in this study are listed in **bold**. Genera preceded with an asterisk were not included in the final combined analysis, but were included in alternative analyses, and are discussed in the text.

COELIADINAE
Bibasis Moore, 1881
Burara Swinhoe, 1893
Allora Waterhouse & Lyell, 1914
Hasora Moore, 1881
Badamia Moore, 1881
Choaspes Moore, 1881

Coeliades Hübner, [1818]
Pyrrhiades Lindsey & Miller, 1965
Pyrrhochalcia Mabille, 1904

PYRRHOPYGINAE
OXYNETRINI
Oxynetra C. Felder & R. Felder, 1862
Cyclopyge Mielke, 2002

PYRRHOPYGINI
Pyrrhopyge Hübner, 1819
****Yanguna*** Watson, 1893
Gunayan Mielke, 2002
Chalypyge Mielke, 2002
Ochropyge Mielke, 2002
Apyrrhothrix Lindsey, 1921
Melanopyge Mielke, 2002
Jonaspyge Mielke, 2002
Creonpyge Mielke, 2002
Cyanopyge Mielke, 2002
Elbella Evans, 1951
Parelbella Mielke, 1995
Pseudocroniades Mielke, 1995
Protelbella Mielke, 1995
Nosphistia Mabille & Boullet, 1908
****Jemadia*** Watson, 1893
****Mimoniades*** Hübner, 1823
Mimardaris Mielke, 2002
Ardaris Watson, 1893
Amenis Watson, 1893
Sarbia Watson, 1893
Metardaris Mabille, 1903
Amysoria Mielke, 2002
Mysoria Watson, 1893
Mysarbia Mielke, 2002
Microceris Watson, 1893
Croniades Mabille, 1903

ZONIINI
Zonia Evans, 1951

PASSOVINI
Azonax Godman & Salvin, 1893
Myscelus Hübner, 1819
Granila Mabille, 1903
Passova Evans, 1951
Aspitha Evans, 1951

PYRGINAE
EUDAMINI
Augiades Group

Phocides Hübner, 1819
Hypocryptothrix Watson, 1893
Tarsoctenus Watson, 1893
Phanus Hübner, 1819
Udranomia Butler, 1870
Drephalys Watson, 1893
Augiades Hübner, 1819
Hyalothyrus Mabille, 1878
Phareas Westwood, 1852
Entheus Hübner, 1819
Cabirus Hübner, 1819

Urbanus Group
Proteides Hübner, 1819
Epargyreus Hübner, 1819
Polygonus Hübner, 1825
Chioides Lindsey, 1921
Aguna Williams, 1927
Cephise Evans, 1952
Typhedanus Butler, 1870
Polythrix Watson, 1893
Heronia Mabille & Boullet, 1912
Chrysoplectrum Watson, 1893
Zestusa Lindsey, 1925
Codatractus Lindsey, 1921
Ridens Evans, 1952
Urbanus Hübner, 1807
Astraptes Hübner, 1819
Narcosius Steinhauser, 1986
Calliades Mabille & Boullet, 1912
Autochton Hübner, 1823
Achalarus Scudder, 1872
Thessia Steinhauser, 1989
Venada Evans, 1952
Thorybes Scudder, 1872
Cabares Godman & Salvin, 1894

Celaenorrhinus Group
“Old World” Subgroup

Euschemon Doubleday, 1846
Chaetocneme C. Felder, 1860
Capila Moore, 1866
Lobocla Moore, 1884

Celaenorrhinus Group
Bungalotis Subgroup

Bungalotis Watson, 1893
Salatis Evans, 1952
Sarmientoia Berg, 1897
Dyscophellus Godman & Salvin, 1893

Celaenorrhinus Group
Nascus Subgroup

Nascus Watson, 1893

Celaenorrhinus Group
Porphyrogenes Subgroup

Porphyrogenes Watson, 1893
Ocyba Lindsey, 1925
Oileides Hübner, 1825

Celaenorrhinus Group
Celaenorrhinus Subgroup

Katreus Watson, 1893
Loxolexis Karsch, 1895
Celaenorrhinus Hübner, 1819
Aurina Evans, 1937

PYRGINI
Tagiades Group
Netrocoryne Subgroup

Netrocoryne C. Felder & R. Felder, 1867
Tapena Moore, 1881
Darpa Moore, 1866
Odina Mabille, 1891
Coladenia Moore, 1881
Pseudocoladenia Shirôzu & Saigusa, 1962
Eagris Guénée, 1863
Calleagris Aurivillius, 1925
Procampta Holland, 1892

Eretis Mabille, 1891
Sarangesa Moore, 1881

Tagiades Group
Tagiades Subgroup

Satarupa Moore, 1866
Seseria Matsumura, 1919
Pintara Evans, 1932
Chamunda Evans, 1949
Daimio Murray, 1875
****Gerosis*** Mabille, 1903
Tagiades Hübner, 1819
Mooreana Evans, 1926
Abraximorpha Elwes & Edwards, 1897
Exometoeca Meyrick, 1888

Tagiades Group
Caprona Subgroup

Ctenoptilum de Nicéville, 1890
****Odontoptilum*** de Nicéville, 1890
Netrobalane Mabille, 1903
Caprona Wallengren, 1857
Leucochitonea Wallengren, 1857
Abantis Hopffer, 1885

Telemiades Group
Telemiades Subgroup

Spathilepia Butler, 1870
Oechydrus Watson, 1893
Jera Lindsey, 1925
Marela Mabille, 1903
Cogia Butler, 1870
Paracogia Mielke, 1977
Telemiades Hübner, 1819
Mimia Evans, 1953
Ectomis Mabille, 1878
Nerula Mabille, 1888

Telemiades Group
Nisoniades Subgroup

Conognathus C. Felder & R. Felder 1862
Arteurotia Butler & H. Druce, 1872
Pseudodrephalys Burns, 1999
Eracon Godman & Salvin, 1894
Cornuphallus Austin, 1997
Spioniades Hübner, 1819
Mictris Evans, 1955
Iliana Bell, 1937
Sophista Plötz, 1879
Polyctor Evans, 1953
Nisoniades Hübner, 1819
Pachyneuria Mabille, 1888
Pellicia Herrich-Schäffer, 1870
Noctuana Bell, 1937
Windia Freeman, 1969a
Morvina Evans, 1953
Myrinia Evans, 1953
Xispia Lindsey, 1925
Ocella Evans, 1953
Cyclosemia Mabille, 1878
Gorgopas Godman & Salvin, 1894

Telemiades Group
Staphylus Subgroup

Viola Evans, 1953
Burca Bell & Comstock, 1948
Bolla Mabille, 1903
Staphylus Godman & Salvin, 1896
Plumbago Evans, 1953
Trina Evans, 1953
Diaeus Godman & Salvin, 1895

Telemiades Group
Quadrus Subgroup
Gorgythion Godman & Salvin, 1896
Ouleus Lindsey, 1925

Zera Evans, 1953
Quadrus Lindsey, 1925

Telemiades Group
Pythonides Subgroup

Gindanes Godman & Salvin, 1895
Pythonides Hübner, 1819
Sostrata Godman & Salvin, 1895
Paches Godman & Salvin, 1895

Telemiades Group
Paramimus Subgroup

Haemactis Mabille, 1903
Atarnes Godman & Salvin, 1897
Milanion Godman & Salvin, 1895
Paramimus Hübner, 1819
Charidia Mabille, 1903

Telemiades Group
Antigonus Subgroup

Potamanaxas Lindsey, 1925
Mylon Godman & Salvin, 1894
Carrhenes Godman & Salvin, 1895
Zobera Freeman, 1970
Clito Evans, 1953
****Xenophanes*** Godman & Salvin, 1895
Onenses Godman & Salvin, 1895
Antigonus Hübner, 1819
Systasea Edwards, 1877
Timochreon Godman & Salvin, 1896
Zopyrion Godman & Salvin, 1896
Anisochoria Mabille, 1876

Erynnis Group

Aethilla Hewitson, 1868
Achlyodes Hübner, 1819
Eantis Boisduval, 1836
Grais Godman & Salvin, 1894
Doberes Godman & Salvin, 1895
Timochares Godman & Salvin, 1896
Anastrus Hübner, 1824
Tosta Evans, 1953
Ebrietas Godman & Salvin, 1896
Helias Fabricius, 1807
Camptopleura Mabille, 1877
Cycloglypha Mabille, 1903
Theagenes Godman & Salvin, 1896
Chiomara Godman & Salvin, 1899
Gesta Evans, 1953
Ephyriades Hübner, 1819
Erynnis Schrank, 1801

Pyrgus Group

Gomalia Moore, 1879
Carcharodus Hübner, 1819
Spialia Swinhoe, 1912
Muschampia Tutt, 1906
Alenia Evans, 1935
Pyrgus Hübner, 1819
Heliopyrgus Herrera, 1957
Heliopetes Billberg, 1820
Pholisora Scudder, 1872
Hesperopsis Dyar, 1905
Celotes Godman & Salvin, 1899
HETEROPTERINAE
Hovala Evans, 1937
Metisella Hemming, 1934
****Tsitana*** Evans, 1937
Lepella Evans, 1937
Leptalina Mabille, 1904
Carterocephalus Lederer, 1852
Heteropterus Duméril, 1806
Barca de Nicéville, 1902
Apostictopterus Leech, 1893
Piruna Evans, 1955
Dardarina Evans, 1937
Butleria Kirby, 1871
Argopteron Watson, 1893
Dalla Mabille, 1904
Freemaniana A. Warren, 2001b

TRAPEZITINAE
Felicena Waterhouse, 1932
Trapezites Hübner, 1819
****Anisynta*** Lower, 1911
****Pasma*** Waterhouse, 1932
Dispar Waterhouse & Lyell, 1914
****Neohesperilla*** Waterhouse & Lyell, 1914
Hewitsoniella Shepard, 1931
Toxidia Mabille, 1891
Signeta Waterhouse & Lyell, 1914
Oreisplanus Waterhouse & Lyell, 1914
Hesperilla Hewitson, 1868
Motasingha Watson, 1893
Antipodia Atkins, 1984
Proeidosa Atkins, 1973
Croitana Waterhouse, 1932
Herimosa Atkins, 1994
Mesodina Mayrick, 1901
Rachelia Hemming, 1964

HESPERIINAE
Astictopterus Group
Astictopterus Subgroup

Astictopterus C. Felder & R. Felder, 1860
Arnetta Watson, 1893

Astictopterus Group
Ampittia Subgroup

Ochus de Nicéville, 1894
Baracus Moore, 1881
Aeromachus de Nicéville, 1890
Prosopalpus Holland, 1896
Ampittia Moore, 1881
Kedestes Watson, 1893
Fulda Evans, 1937
Galerga Mabille, 1898
Gorgyra Holland, 1896
Gyrogra Lindsey & Miller, 1965

Astictopterus Group
Halpe Subgroup

Sebastonyma Watson, 1893
Sovia Evans, 1949
Parasovia Devyatkin, 1996
Pedesta Hemming, 1934
Onryza Watson, 1893
Thoressa Swinhoe, 1913
Halpe Moore, 1878
Pithauria Moore, 1878

Isoteinon Group

Isoteinon C. Felder & R. Felder, 1862
Actinor Watson, 1893
Eogenes Mabille, 1909

Ceratrichia Group

Teniorhinus Holland, 1892
Ceratrichia Butler, 1870
Pardaleodes Butler, 1870
Ankola Evans, 1937
Xanthodisca Aurivillius, 1925
Acada Evans, 1937
Parosmodes Holland, 1896
Rhabdomantis Holland, 1896
Osmodes Holland, 1892
Osphantes Holland, 1896

Acleros Group

Paracleros Berger, 1896
Acleros Mabille, 1885
Semalea Holland, 1896
Hypoleucis Mabille, 1891
Meza Hemming, 1939
Paronymus Aurivillius, 1925
Andronymus Holland, 1896

Ploetzia Group

Malaza Mabille, 1904
Miraja Evans, 1937
Perrotia Oberthür, 1916
Ploetzia Saalmüller, 1884
Moltena Evans, 1937
Chondrolepis Mabille, 1904
Zophopetes Mabille, 1904
Gamia Holland, 1896
Artitropa Holland, 1896
Mopala Evans, 1937
****Gretna*** Evans, 1937
****Pteroteinon*** Watson, 1893
Leona Evans, 1937
Caenides Holland, 1896
Monza Evans, 1937

Ancistroides Group

Iambrix Watson, 1893
Idmon de Nicéville, 1895
****Koruthaialos*** Watson, 1893
Psolos Staudinger, 1889

Stimula de Nicéville, 1898
Ancistroides Butler, 1874
****Notocrypta*** de Nicéville, 1889
Udaspes Moore, 1881

Plastingia Group
Plastingia Subgroup

Praescobura Devyatkin, 2002
Scobura Elwes & Edwards, 1897
Suada de Nicéville, 1895
Suastus Moore, 1881
Cupitha Moore, 1884
Zographetus Watson, 1893
Oerane Elwes & Edwards, 1897
Hyarotis Moore, 1881
Quedara Swinhoe, 1919
Isma Distant, 1886
Xanthoneura Eliot, 1978
Plastingia Butler, 1870
Salanoemia Eliot, 1978
****Pemara*** Eliot, 1978
****Pyroneura*** Eliot, 1978
Pseudokerana Eliot, 1978
Lotongus Distant, 1886

Plastingia Group
Erionota Subgroup

Zela de Nicéville, 1895
Gangara Moore, 1881
Erionota Mabille, 1878
Ilma Swinhoe, 1905
Ge de Nicéville, 1895
Matapa Moore, 1881
Pudicitia de Nicéville, 1895

Plastingia Group
Unkana Subgroup

Unkana Distant, 1886
Hidari Distant, 1886
Eetion de Nicéville, 1895
Acerbas de Nicéville, 1895
Pirdana Distant, 1886
Pseudopirdana Chiba & Tsukiyama, 1994
Creteus de Nicéville, 1895

Plastingia Group
Prada Subgroup

Prada Evans, 1949
Tiacellia Evans, 1949

Vinius Group

Falga Mabille, 1898
Synapte Mabille, 1904
Lento Evans, 1955
Levina Evans, 1955
Zariaspes Godman, 1900
Anthoptus Bell, 1942
Corticea Evans, 1955
Zalomes Bell, 1947
Wahydra Steinhauser, 1991
Cantha Evans, 1955
Vinius Godman, 1900
Vinpeius Austin, 1997
Pheraeus Godman, 1900
Misius Evans, 1955
Molo Godman, 1900
Racta Evans, 1955
Pyrrhocalles Mabille, 1904

Apaustus Group
Apaustus Subgroup

Apaustus Hübner, 1819
Callimormus Scudder, 1872
Radiatus Mielke, 1968
Peba Mielke, 1968
Eutocus Godman, 1901
Virga Evans, 1955
Eprius Godman, 1901
Mnasicles Godman, 1901
Ludens Evans, 1955
Methionopsis Godman, 1901
Panca Evans, 1955
Sodalia Evans, 1955
Mnestheus Godman, 1901
Artines Godman, 1901
Flaccilla Godman, 1901
Mnaseas Godman, 1901
Inglorius Austin, 1997

Apaustus Group
Phanes Subgroup

Gallio Evans, 1955
Methion Godman, 1900
Thargella Godman, 1900
Venas Evans, 1955
Pamba Evans, 1955
Saniba Mielke & Casagrande, 2003
Repens Evans, 1955
Lucida Evans, 1955
Phanes Godman, 1901

Apaustus Group
Cymaenes Subgroup

Vidius Evans, 1955
Igapophilus Mielke, 1980
Monca Evans, 1955
Nastra Evans, 1955
Cymaenes Scudder, 1872
Vehilius Godman, 1900
Mnasilus Godman, 1900
Sucova Evans, 1955
Mnasinous Godman, 1900
Mnasitheus Godman, 1900
Moeris Godman, 1900
Remella Hemming, 1939
****Parphorus*** Godman, 1900

Apaustus Group
Lerema Subgroup

Molla Evans, 1955
Papias Godman, 1900
Propapias Mielke, 1992
Cobalopsis Godman, 1900
Arita Evans, 1955
Lerema Scudder, 1872
Morys Godman, 1900
Cumbre Evans, 1955
Adlerodea Hayward, 1940

Psoralis Mabille, 1904
Tigasis Godman, 1900
Eutychide Godman, 1900
Onophas Godman, 1900

Apaustus Group
Vettius Subgroup

Vettius Godman, 1901
Paracarystus Godman, 1900
Turesis Godman, 1901
Thoon Godman, 1900
Justinia Evans, 1955
Lamponia Evans, 1955
Naevolus Hemming, 1939

Carystus Group

Miltomiges Mabille, 1903
Styriodes Schaus, 1913
Dion Godman, 1901
Enosis Mabille, 1889
Vertica Evans, 1955
Ebusus Evans, 1955
Evansiella Hayward, 1948
Argon Evans, 1955
Cobaloides Hayward, 1939
Sacrator Evans, 1955
Megaleas Godman, 1901
Lychnuchus Hübner, 1831
Talides Hübner, 1819
Tromba Evans, 1955
Nyctus Mabille, 1891
Turmada Evans, 1955
Synale Mabille, 1904
Carystus Hübner, 1819
Telles Godman, 1900
Tisias Godman, 1901
Moeros Evans, 1955
Cobalus Hübner, 1819
Dubiella Evans, 1936
Carystina Evans, 1955
Tellona Evans, 1955
Damas Godman, 1901
Orphe Godman, 1901
Carystoides Godman, 1901
Lychnuchoides Godman, 1901
Perichares Scudder, 1872
Orses Godman, 1901
Alera Mabille, 1891
Lycas Godman, 1901

Phlebodes Group
Phlebodes Subgroup

Saturnus Evans, 1955
Phlebodes Hübner, 1819
Joanna Evans, 1955
Punta Evans, 1955
Bruna Evans, 1955
Quinta Evans, 1955
Cynea Evans, 1955
Rhinthon Godman, 1900
****Mucia*** Godman, 1900
Penicula Evans, 1955

Phlebodes Group
Oeonus Subgroup

Decinea Evans, 1955
Oeonus Godman, 1900
Cyclosma Draudt, 1923
Caligulana Bell, 1942
Orthos Evans, 1955
Conga Evans, 1955
Holguinia Evans, 1955

Hesperia Group
Thymelicus Subgroup

Ancyloxypha C. Felder, [1863]
Oarisma Scudder, 1872
Copaeodes Speyer, 1877
Adopaeoides Godman, 1900
Thymelicus Hübner, 1819

Hesperia Group
Hesperia Subgroup

Hylephila Billberg, 1820
Pseudocopaeodes Skinner & Williams, 1923
Stinga Evans, 1955
Hesperia Fabricius, 1793
Appia Evans, 1955
Linka Evans, 1955
Polites Scudder, 1872
Wallengrenia Berg, 1897
Pompeius Evans, 1955
Atalopedes Scudder, 1872
Atrytone Scudder, 1872
Problema Skinner & Williams, 1924
Ochlodes Scudder, 1872
Neochlodes Austin & DeVries, 2001
Buzyges Godman, 1900
Onespa Steinhauser, 1974
Poanes Scudder, 1872
Paratrytone Godman, 1900
Choranthus Scudder, 1872
Parachoranthus Miller, 1965
Anatrytone Dyar, 1905
Quasimellana Burns, 1994a
Librita Evans, 1955

Hesperia Group
Phemiades Subgroup

Euphyes Scudder, 1872
Arotis Mabille, 1904
Libra Evans, 1955
Hansa Evans, 1955
Chalcone Evans, 1955
Serdis Mabille, 1904
Metron Godman, 1900
Propertius Evans, 1955
Phemiades Hübner, 1819
Asbolis Mabille, 1904

Lerodea Group

Atrytonopsis Godman, 1900
Amblyscirtes Scudder, 1872
Notamblyscirtes Scott, 2006
****Lerodea*** Scudder, 1872
Oligoria Scudder, 1872

Calpodes Group
Calpodes Subgroup

Calpodes Hübner, 1819
Panoquina Hemming, 1934
Zenis Godman, 1900
Tirynthoides Bell, 1940

Calpodes Group
Niconiades Subgroup

Tirynthia Godman, 1900
Nyctelius Hayward, 1948
Thespieus Godman, 1900
Vacerra Godman, 1900
Jongiana Mielke & Casagrande, 2002
Lindra Evans,1955
Oxynthes Godman, 1900
Niconiades Hübner, 1821
***Halotus** Godman, 1900

Calpodes Group
Aides Subgroup

Aides Billberg, 1820
***Xeniades** Godman, 1900
Cravera de Jong, 1983

Calpodes Group
Thracides Subgroup

Saliana Evans, 1955
Thracides Hübner, 1819
Neoxeniades Hayward, 1938
Aroma Evans, 1955

Calpodes Group
Chloeria Subgroup

Chloeria Mabille, 1904

Calpodes Group
Pseudosarbia Subgroup

Pyrrhopygopsis Godman, 1901
Pseudosarbia Berg, 1897

Taractrocera Group

Taractrocera Butler, 1870
Ocybadistes Heron, 1894

Suniana Evans, 1934
Oriens Evans, 1932
Potanthus Scudder, 1872
Arrhenes Mabille, 1904
Telicota Moore, 1881
Cephrenes Waterhouse & Lyell, 1914
Pastria Evans, 1949
Banta Evans, 1949
Kobrona Evans, 1935
Sabera Swinhoe, 1908
Mimene Joicey & Talbot, 1917

Gegenes Group

Prusiana Evans, 1937
Melphina Evans, 1937
Fresna Evans, 1937
Platylesches Holland, 1896
Brusa Evans, 1937
Zenonia Evans, 1935
Gegenes Hübner, 1819
Parnara Moore, 1881
Borbo Evans, 1949
Pelopidas Walker, 1870
Polytremis Mabille, 1904
Baoris Moore, 1881
***Caltoris** Swinhoe, 1893
Iton de Nicéville, 1895

MEGATHYMINAE
MEGATHYMINI
Megathymus Scudder, 1872
Stallingsia Freeman, 1959

AEGIALINI
Aegiale C. Felder & R. Felder, 1860
Turnerina Freeman, 1959

AGATHYMINI
Agathymus Freeman, 1959

FOSSIL GENERA
Pamphilites Scudder, 1875
Thanatites Scudder, 1875

Appendix 2

List of Hesperiidae and outgroups sampled in this study, with abbreviated locality information and GenBank accession numbers

				GenBank accession no.		
Higher taxon	Genus and species	Voucher no. and location	Locality and other voucher codes	*wingless*	COI	Ef-1α
PAPILIONIDAE	*Papilio machaon*	FS.a-27	From GenBank, collection locality not stated	AY569124	AF044006	AF044819
PIERIDAE	*Colias eurytheme*	FS.b-543	From GenBank, collection locality not stated	AY569040	AF044024	AF173400
LYCAENIDAE	*Lycaena helloides*	NP99W131	From GenBank, collection locality not stated	DQ018886	DQ018948	DQ018915
RIODINIDAE	*Emesis mandana*	PDV94T022	From GenBank, collection locality not stated	DQ018888	DQ018950	DQ018917
DANAIDAE	*Danaus plexippus*	NW108-22	From GenBank, collection locality not stated	DQ018891	DQ018954	DQ018921
HESPERIIDAE						
COELIADINAE						
	Bibasis sena	633-MCZ	THAILAND: Jom Tien DL03X004	EU363904	EU364302	EU364097
	Burara aquilina	383-ADW	JAPAN: Hokkaido	EU363905	EU364303	EU364098
	Hasora khoda	97-ADW	AUSTRALIA: NSW: Dudley	DQ018871	DQ018930	DQ18901
	Badamia exclamationis	370-ADW	VIETNAM: Tay Ninh Prov.	EU363903	EU364301	EU364096
	Choaspes stigmata	595-MCZ	MALAYSIA: Sarawak NP95Y077	EU363906	EU364304	EU364099
	Coeliades forestan	533-ADW	GHANA: Ashanti Region DM02-002	EU363907	EU364305	EU364100
PYRRHOPYGINAE						
Pyrrhopygini	*Pyrrhopyge zenodorus*	516-ADW	COSTA RICA: Guanacaste 01-SRNP-4547	EU363910	EU364308	EU364103
	Apyrrothrix araxes	628-MCZ	USA: Arizona: Cochise Co. DC98U664	EU363908	EU364306	EU364101
	Creonpyge creon	626-MCZ	COSTA RICA: San Jose Prov. RE01H111	EU363909	EU364307	EU364102
	Elbella scylla	523-ADW	COSTA RICA: Guanacaste 01-SRNP-12006	EU363911	EU364309	EU364104
	Parelbella macleannani	525-ADW	COSTA RICA: Guanacaste 01-SRNP-462	EU363912	EU364310	EU364105
	Sarbia xanthippe	426-ADW	BRAZIL: Paraná: Campo Largo	EU363913	EU364311	EU364106
	Mysoria ambigua	138-ADW	COSTA RICA: Guanacaste Prov.: ACG	DQ018874	DQ018933	DQ018904
Passovini	*Myscelus belti*	638-ADW	COSTA RICA: Guanacaste 02-SRNP-14661	EU363915	EU364313	EU364108
	Passova gellias	437-ADW	COSTA RICA: Guanacaste 01-SRNP-283	EU363914	EU364312	EU364107
PYRGINAE						
Eudamini						
Augiades Group	*Phocides lilea*	441-ADW	COSTA RICA: Guanacaste 01-SRNP-4551	EU363916	EU364314	EU364109
	Udranomia kikkawai	508-ADW	COSTA RICA: Guanacaste 01-SRNP-12035	EU363917	EU364315	EU364110
	Drephalys kidonoi	454-ADW	COSTA RICA: Guanacaste 01-SRNP-12339	EU363919	EU364317	EU364112
	Hyalothyrus mimicus	65-ADW	ECUADOR: Napo Prov.: Yasuni	EU363918	EU364316	EU364111
Urbanus Group	*Proteides mercurius*	139-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363920	EU364318	EU364113
	Polygonus leo	147-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363921	EU364319	EU364114
	Chioides catillus	151-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363922	EU364320	EU364115
	Aguna asander	140-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363923	EU364321	EU364116
	Typhedanus ampyx	143-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363924	EU364322	EU364117
	Zestusa elwesi	504-ADW	MEXICO: Guanajuato: vic. Santa Rosa	EU363926	EU364324	EU364119
	Codatractus melon	187-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363925	EU364323	EU364118
	Urbanus dorantes	280-ADW	COSTA RICA: Guanacaste Prov.: ACG	DQ018870	DQ018929	DQ018900
	Urbanus simplicius	59-ADW	ECUADOR: Napo Prov.: Yasuni	EU363927	EU364325	EU364120
	Astraptes "fulgerator"	142-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363928	EU364326	EU364121
	Narcosius colossus	527-ADW	COSTA RICA: Guanacaste 01-SRNP-12043	EU363929	EU364327	EU364122
	Calliades zeutus	529-ADW	COSTA RICA: Guanacaste 01-SRNP-9181	EU363930	EU364328	EU364123
	Autochton longipennis	67-ADW	ECUADOR: Napo Prov.: Yasuni	EU363931	EU364329	EU364124

Appendix 2
Continued

Higher taxon	Genus and species	Voucher no. and location	Locality and other voucher codes	GenBank accession no. *wingless*	COI	Ef-1α
	Achalarus albociliatus	186-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363932	EU364330	EU364125
	Thorybes pylades	27-ADW	USA: Arizona: Cochise Co.	EU363933	EU364331	EU364126
	Cabares potrillo	499-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363934	EU364332	EU364127
Celaenorrhinus Group	*Bungalotis erythus*	403-ADW	COSTA RICA: Guanacaste 01-SRNP-9143	EU363935	EU364333	EU364128
	Dyscophellus phraxanor	407-ADW	COSTA RICA: Guanacaste 01-SRNP-496	EU363936	EU364334	EU364129
	Nascus paulliniae	639-ADW	COSTA RICA: Guanacaste 02-SRNP-15760	EU363937	EU364335	EU364130
	Ocyba calathana	456-ADW	COSTA RICA: Guanacaste 01-SRNP-9158	EU363938	EU364336	EU364131
	Euschemon rafflesia	85-ADW	AUSTRALIA: NSW: Port Macquarie	EU363939	EU364337	EU364132
	Lobocla liliana	597-MCZ	THAILAND: Chiang Mai; DL02P688	EU363940	EU364338	EU364133
	Celaenorrhinus leona	551-ADW	GHANA: Ashanti Region DM02-088	EU363941	EU364339	EU364134
	Celaenorrhinus eligius	137-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363942	EU364340	EU364135
Pyrgini						
Tagiades Group	*Netrocoryne repanda*	99-ADW	AUSTRALIA: NSW: Mt. Sugarloaf	EU363943	EU364341	EU364136
	Darpa striata	589-MCZ	MALAYSIA: Pahang NP95Y230	EU363950	EU364348	EU364143
	Pseudocoladenia dan	603-MCZ	THAILAND: Yala DL02P627	EU363948	EU364346	EU364141
	Eagris tetrastigma	545-ADW	GHANA: Ashanti Region DM02-060	EU363945	EU364343	EU364138
	Eretis plistonicus	572-ADW	GHANA: Ashanti Region	EU363946	EU364344	EU364139
	Sarangesa bouvieri	546-ADW	GHANA: Ashanti Region DM02-133	EU363947	EU364345	EU364140
	Daimio tethys	250-ADW	JAPAN: Shizuoka Pref.		EU364347	EU364142
	Daimio tethys	388-ADW	JAPAN: Fukuoka Pref.	EU363949		
	Tagiades flesus	542-ADW	GHANA: Ashanti Region DM02-084	EU363944	EU364342	EU364137
Telemiades Group	*Spathilepia clonius*	141-ADW	COSTA RICA: Guanacaste Prov: ACG	EU363951	EU364349	EU364144
	Cogia calchas	78-ADW	ECUADOR: Napo Prov.: Yasuni	EU363952	EU364350	EU364145
	Telemiades fides	509-ADW	COSTA RICA: Guanacaste 01-SRNP-12165	EU363953	EU364351	EU364146
	Eracon lachesis	457-ADW	COSTA RICA: Guanacaste 01-SRNP-4809	EU363954	EU364352	EU364147
	Pachyneuria lineatopunctata	481-ADW	BRAZIL: Rondonia: Candeias do Jamari	EU363956	EU364354	EU364149
	Cyclosemia anastomosis	625-MCZ	COSTA RICA: Cartago Prov. RE01H190	EU363955	EU364353	EU364148
	Viola minor	342-ADW	BRAZIL: Paraná: Campo Largo	EU363957	EU364355	EU364150
	Staphylus ceos	82-ADW	USA: Arizona: Cochise Co.	EU363958	EU364356	EU364151
	Gorgythion begga	180-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363959	EU364357	EU364152
	Quadrus cerialis	510-ADW	COSTA RICA: Guanacaste 01-SRNP-9251	EU363960	EU364358	EU364153
	Pythonides jovianus	511-ADW	COSTA RICA: Guanacaste 01-SRNP-18	EU363961	EU364359	EU364154
	Sostrata nordica	637-ADW	COSTA RICA: Guanacaste 02-SRNP-13762	EU363962	EU364360	EU364155
	Atarnes sallei	188-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363964	EU364362	EU364157
	Milanion marciana	636-ADW	COSTA RICA: Guanacaste 02-SRNP-7685	EU363963	EU364361	EU364156
	Mylon pelopidas	176-ADW	COSTA RICA: Guanacaste Prov: ACG	EU363966	EU364364	EU364159
	Clito aberrans	459-ADW	COSTA RICA: Guanacaste 01-SRNP-12029	EU363965	EU364363	EU364158
	Antigonus erosus	179-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363967	EU364365	EU364160
	Systasea zampa	614-MCZ	USA: Arizona: Cochise Co.	EU363968	EU364366	EU364161
	Zopyrion sandace	192-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363969	EU364367	EU364162
Erynnis Group	*Aethilla lavochrea*	521-ADW	COSTA RICA: Guanacaste 01-SRNP-9157	EU363971	EU364369	EU364164
	Achlyodes busirus	54-ADW	ECUADOR: Napo Prov.: Yasuni	EU363970	EU364368	EU364163
	Timochares trifasciata	177-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363972	EU364370	EU364165
	Ebrietas anacreon	485-ADW	BRAZIL: Rondonia: Candeias do Jamari	EU363976	EU364374	EU364169
	Ebrietas infanda	66-ADW	ECUADOR: Napo Prov.: Yasuni	EU363977	EU364375	EU364170

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Higher taxon	Genus and species	Voucher no. and location	Locality and other voucher codes	GenBank accession no.		
				wingless	COI	Ef-1α
	Helias phalaenoides	435-ADW	BRAZIL: Paraná: Pontal do Paraná	EU363975	EU364373	EU364168
	Camptopleura auxo	81-ADW	ECUADOR: Napo Prov.: Yasuni	EU363974	EU364372	EU364167
	Theagenes dichrous	483-ADW	BRAZIL: Paraná: Campo Largo	EU363973	EU364371	EU364166
	Gesta invisus	189-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU363978	EU364376	EU364171
	Erynnis afranius	52-ADW	USA: Colorado: Douglas Co.	EU363980	EU364378	EU364173
	Erynnis horatius	39-ADW	USA: Colorado: Douglas Co.		EU364377	EU364172
	Erynnis horatius	40-ADW	USA: Colorado: Douglas Co.	EU363979		
Pyrgus Group	*Carcharodus alceae*	640-ADW	MACEDONIA: Babuna	EU363982	EU364380	EU364175
	Spialia sertorius	390-ADW	FRANCE: Aude: Villegly	EU363983	EU364381	EU364176
	Alenia namaqua	619-MCZ	SOUTH AFRICA: AAM98V083	EU363981	EU364379	EU364174
	Pyrgus communis	2-ADW	USA: Colorado: Douglas Co.		EU364384	EU364179
	Pyrgus communis	6-ADW	USA: Colorado: Douglas Co.	EU363986		
	Pyrgus ruralis	10-ADW	USA: Oregon: Benton Co.	EU363984	EU364382	EU364177
	Pyrgus scriptura	49-ADW	USA: Colorado: Douglas Co.	EU363985	EU364383	EU364178
	Heliopetes alana	74-ADW	ECUADOR: Napo Prov.: Yasuni	EU363987	EU364385	EU364180
	Pholisora catullus	12-ADW	USA: Colorado: Douglas Co.	EU363988	EU364386	EU364181
	Celotes nessus	254-ADW	USA: Arizona: Pima Co.	EU363989	EU364387	EU364182
HETEROPTERINAE						
	Metisella metis	631-ADW	SOUTH AFRICA: Cape Town	EU363994	EU364392	EU364187
	Carterocephalus palaemon	227-ADW	USA: Oregon: Jefferson Co.	EU363990		
	Carterocephalus palaemon	228-ADW	USA: Oregon: Jefferson Co.		EU364388	EU364183
	Piruna aea	275-ADW	USA: Arizona: Santa Cruz Co.	EU363991	EU364389	EU364184
	Dardarina dardaris	198-ADW	COSTA RICA: Guanacaste Prov: ACG	EU363993	EU364391	EU364186
	Butleria bissexguttatus	629-AVZB	CHILE: Llanquihue Prov. CH-10B-5	EU363992	EU364390	EU364185
TRAPEZITINAE						
	Trapezites symmomus	89-ADW	AUSTRALIA: NSW: Dudley	DQ018873	DQ018932	DQ018903
	Dispar compacta	100-ADW	AUSTRALIA: NSW: Bennets Green		EU364402	EU364197
	Toxidia doubledayi	88-ADW	AUSTRALIA: NSW: Bennets Green	EU364001	EU364400	EU364195
	Toxidia peron	86-ADW	AUSTRALIA: NSW: Mt. Sugarloaf	EU364002	EU364401	EU364196
	Signeta flammeata	304-ADW	AUSTRALIA: NSW: Barrington Tops	EU363998	EU364397	EU364192
	Oreisplanus perornata	308-ADW	AUSTRALIA: VICTORIA: Grampian Mts.	EU363996	EU364394	EU364189
	Hesperilla donnysa	105-ADW	AUSTRALIA: NSW: Bennets Green	EU363997	EU364395	EU364190
	Hesperilla ornata	101-ADW	AUSTRALIA: NSW: Bennets Green		EU364396	EU364191
	Motasingha trimaculata	312-ADW	AUSTRALIA: NSW: Clarence	EU364000	EU364399	EU364194
	Antipodia atralba	616-MCZ	AUSTRALIA: W AUST: AAM97U336	EU363995	EU364393	EU364188
	Mesodina aeluropis	116-ADW	AUSTRALIA: NSW: Clarence	EU363999	EU364398	EU364193
HESPERIINAE						
Astictopterus Group	*Astictopterus jama*	337-ADW	VIETNAM: Tay Ninh Prov.	EU364012	EU364412	EU364207
	Ampittia discorides	615-MCZ	THAILAND: nr. Khorat DL00Q188	EU364006	EU364406	EU364201
	Kedestes barberae	632-ADW	SOUTH AFRICA: Groot Winterberg	EU364007	EU364407	EU364202
	Sovia albipectus	339-ADW	VIETNAM: Tay Ninh Prov.	EU364014	EU364414	EU364209
	Thoressa varia	167-ADW	JAPAN: Tokyo Pref.	EU364015	EU364415	EU364210
	Halpe porus	598-MCZ	THAILAND: Chiang Mai DL02P713	EU364013	EU364413	EU364208
Isoteinon Group	*Isoteinon lamprospilus*	165-ADW	JAPAN: Yamanashi Pref.	EU364016	EU364416	EU364211
Ceratrichia Group	*Ceratrichia clara*	548-ADW	GHANA: Ashanti Region DM02-049	EU364017	EU364417	EU364212

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Higher taxon	Genus and species	Voucher no. and location	Locality and other voucher codes	GenBank accession no.		
				wingless	COI	Ef-1α
	Xanthodisca astrape	550-ADW	GHANA: Ashanti Region DM02-019	EU364019	EU364419	EU364214
	Osmodes lindseyi	549-ADW	GHANA: Ashanti Region DM02-073	EU364018	EU364418	EU364213
Acleros Group	*Paracleros biguttulus*	553-ADW	GHANA: Ashanti Region DM02-062	EU364005	EU364405	EU364200
	Meza meza	562-ADW	GHANA: Ashanti Region DM02-021	EU364004	EU364404	EU364199
	Andronymus evander	555-ADW	GHANA: Ashanti Region DM02-147	EU364003	EU364403	EU364198
Ploetzia Group	*Gamia shelleyi*	573-ADW	GHANA: Ashanti Region	EU364029	EU364430	EU364225
	Caenides dacela	566-ADW	GHANA: Ashanti Region DM02-020	EU364028	EU364429	EU364224
Ancistroides Group	*Iambrix salsala*	396-ADW	MALAYSIA: Selangor: Ampang Ukay	EU364010	EU364410	EU364205
	Idmon obliquans	394-ADW	MALAYSIA: Selangor: Ampang Ukay	EU364011	EU364411	EU364206
	Ancistroides nigrita	593-MCZ	THAILAND: Phang Nga DL02Q783	EU364008	EU364408	EU364203
	Ancistroides nigrita	400-ADW	MALAYSIA: Johor: Endau Rompin N. P.	EU364009	EU364409	EU364204
Plastingia Group	*Suada swerga*	336-ADW	VIETNAM: Tay Ninh Prov.		EU364426	EU364221
	Suastus minutus	594-MCZ	THAILAND: Pang Nga DL02Q784	EU364026	EU364427	EU364222
	Hyarotis adrastus	605-MCZ	THAILAND: Yala DL02P667	EU364023	EU364423	EU364218
	Plastingia naga	331-ADW	VIETNAM: Tay Ninh Prov.	EU364025	EU364425	EU364220
	Lotongus calathus	338-ADW	VIETNAM: Tay Ninh Prov.	EU364024	EU364424	EU364219
	Zela excellens	607-MCZ	THAILAND: Trang DL02N783	EU364027	EU364428	EU364223
	Gangara thyrsis	608-MCZ	THAILAND: Trang DL02N798	EU364021	EU364421	EU364216
	Unkana mytheca	399-ADW	MALAYSIA: Johor: Endau Rompin N. P.	EU364020	EU364420	EU364215
	Hidari irava	602-MCZ	THAILAND: Had Yai DL02P621	EU364022	EU364422	EU364217
Vinius Group	*Synapte silius*	634-ADW	COSTA RICA: Guanacaste 02-SNRP-13683	EU364030	EU364431	EU364226
	Lento xanthina	195-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364034	EU364435	EU364230
	Anthoptus epictetus	63-ADW	ECUADOR: Napo Prov.: Yasuni	EU364031	EU364432	EU364227
	Corticea corticea	173-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364032	EU364433	EU364228
	Vinius letis	480-ADW	BRAZIL: Santa Catarina: Santa Cecilia	EU364033	EU364434	EU364229
Apaustus Group	*Callimormus radiola*	80-ADW	ECUADOR: Napo Prov.: Yasuni	EU364035	EU364436	EU364231
	Virga austrinus	341-ADW	BRAZIL: Paraná: Campo Largo		EU364439	EU364234
	Mnasicles hicetaon	209-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364036	EU364437	EU364232
	Sodalia coler	491-ADW	BRAZIL: Paraná: Pontal do Paraná	EU364037	EU364438	EU364233
	Lucida ranesus	350-ADW	BRAZIL: Santa Catarina: Santa Cecilia	EU364038	EU364440	EU364235
	Vidius catarinae	349-ADW	BRAZIL: Santa Catarina: Moro da Igreja	EU364044	EU364446	EU364241
	Monca crispinus	507-ADW	BELIZE: Cayo: Las Cuevas Research Sta.	EU364039	EU364441	EU364236
	Cymaenes alumna	77-ADW	ECUADOR: Napo Prov.: Yasuni	EU364041	EU364443	EU364238
	Vehilius putus	79-ADW	ECUADOR: Napo Prov.: Yasuni	EU364042	EU364444	EU364239
	Mnasilus allubita	267-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364040	EU364442	EU364237
	Remella rita	501-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364043	EU364445	EU364240
	Papias phainis	210-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364048	EU364450	EU364245
	Morys valda	208-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364050	EU364452	EU364247
	Morys micythus	206-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364049	EU364451	EU364246
	Cumbre belli	343-ADW	BRAZIL: Paraná: Campo Largo	EU364045	EU364447	EU364242
	Vettius artona	477-ADW	BRAZIL: Paraná: Curitiba		EU364453	EU364248
	Eutychide olympia	475-ADW	BRAZIL: Paraná: Pontal do Paraná	EU364046	EU364448	EU364243
	Eutychide paria	460-ADW	COSTA RICA: Guanacaste 01-SRNP-823	EU364047	EU364449	EU364244

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Higher taxon	Genus and species	Voucher no. and location	Locality and other voucher codes	GenBank accession no.		
				wingless	COI	Ef-1α
Carystus Group	*Talides sinois*	512-ADW	COSTA RICA: Guanacaste 01-SRNP-923	EU364054	EU364457	EU364252
	Dubiella belpa	458-ADW	COSTA RICA: Guanacaste 01-SRNP-4855	EU364051	EU364454	EU364249
	Perichares philetes	448-ADW	COSTA RICA: Guanacaste 01-SRNP-486	EU364053	EU364456	EU364251
	Orses cynisca	410-ADW	COSTA RICA: Guanacaste 00-SRNP-22172	EU364052	EU364455	EU364250
Phlebodes Group	*Saturnus metonidia*	346-ADW	BRAZIL: Paraná: Pontal do Paraná	EU364056	EU364459	EU364254
	Penicula roppai	474-ADW	BRAZIL: Paraná: Pontal do Paraná	EU364055	EU364458	EU364253
	Decinea decinea	468-ADW	BRAZIL: Paraná: Pontal do Paraná		EU364462	EU364257
	Caligulana caligula	472-ADW	BRAZIL: Santa Catarina: Serra do Panelho	EU364057	EU364460	EU364255
	Conga chydaea	204-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364058	EU364461	EU364256
Hesperia Group	*Ancyloxypha numitor*	611-MCZ	USA: Massachusetts: Middlesex Co. CA94N009	AF233564	EU364463	EU364258
	Oarisma garita	20-ADW	USA: Colorado: Douglas Co.	EU364059	EU364464	EU364259
	Copaeodes aurantiaca	268-ADW	USA: Arizona: Santa Cruz Co.	EU364060	EU364465	EU364260
	Hylephila phyleus	630-AVZB	CHILE: Malleco Prov., CH-40-6	EU364062	EU364467	EU364262
	Pseudocopaeodes eunus	229-ADW	USA: California: Inyo Co.	EU364061	EU364466	EU364261
	Stinga morrisoni	94-ADW	MEXICO: Mexico: Ixtaccihuatl	EU364063	EU364468	EU364263
	Hesperia leonardus	42-ADW	USA: Colorado: Douglas Co.	EU364065	EU364470	EU364265
	Appia appia	344-ADW	BRAZIL: Paraná: Campo Largo	EU364064	EU364469	EU364264
	Polites themistocles	14-ADW	USA: Colorado: Douglas Co.	EU364066	EU364471	EU364266
	Pompeius pompeius	60-ADW	ECUADOR: Napo Prov.: Yasuni	EU364068	EU364473	EU364268
	Atalopedes campestris	220-ADW	USA: Oregon: Benton Co.	EU364067	EU364472	EU364267
	Ochlodes sylvanoides	50-ADW	USA: Colorado: Douglas Co.	DQ018872	DQ018931	DQ018902
	Poanes taxiles	21-ADW	USA: Colorado: Douglas Co.	EU364069	EU364474	EU364269
	Anatrytone logan	37-ADW	USA: Colorado: Douglas Co.		EU364475	EU364270
	Euphyes vestris	23-ADW	USA: Colorado: Douglas Co.		EU364477	EU364272
	Libra aligula	352-ADW	BRAZIL: Paraná: Curitiba	EU364071	EU364478	EU364273
	Hansa devergens	351-ADW	BRAZIL: Santa Catarina: Santa Cecilia	EU364070	EU364476	EU364271
Lerodea Group	*Amblyscirtes exoteria*	30-ADW	USA: Arizona: Cochise Co.	EU364072	EU364479	EU364274
	Amblyscirtes simius	31-ADW	USA: Colorado: Las Animas Co.	EU364073	EU364480	EU364275
Calpodes Group	*Calpodes ethlius*	144-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364086	EU364494	EU364289
	Panoquina hecebolus	506-ADW	BELIZE: Cayo: Las Cuevas Research Sta.		EU364496	EU364291
	Panoquina ocola	174-ADW	COSTA RICA: Guanacaste Prov.: ACG		EU364495	EU364290
	Nyctelius nyctelius	160-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364089	EU364499	EU364294
	Thespieus macareus	502-ADW	COSTA RICA: Guanacaste Prov.: ACG	EU364090	EU364500	EU364295
	Lindra brasus	348-ADW	BRAZIL: Paraná: Pontal do Paraná	EU364087	EU364497	EU364292
	Niconiades xanthaphes	635-ADW	COSTA RICA: Guanacaste 02-SRNP-30346	EU364088	EU364498	EU364293
	Saliana esperi	514-ADW	COSTA RICA: Guanacaste 01-SRNP-653	EU364091	EU364501	EU364296
	Thracides phidon	451-ADW	COSTA RICA: Guanacaste 01-SRNP-1153	EU364092	EU364502	EU364297
	Pyrrhopygopsis crates	64-ADW	ECUADOR: Napo Prov.: Yasuni	EU364093	EU364503	EU364298

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Higher taxon	Genus and species	Voucher no. and location	Locality and other voucher codes	GenBank accession no.		
				wingless	COI	Ef-1α
Taractrocera Group	*Taroctrocera papyria*	293-ADW	AUSTRALIA: NSW: Catherine Hill Bay	EU364074	EU364481	EU364276
	Ocybadistes walkeri	90-ADW	AUSTRALIA: NSW: Mt. Sugarloaf	EU364075	EU364482	EU364277
	Suniana sunias	379-ADW	PAPUA NEW GUINEA: Haia	EU364076	EU364483	EU364278
	Suniana sunias	326-ADW	AUSTRALIA: NSW: Caves Beach		EU364484	EU364279
	Potanthus sp.	392-ADW	MALAYSIA: Johor: Endau Rompin N. P.	EU364077	EU364485	EU364280
	Arrhenes dschilus	311-ADW	AUSTRALIA: N QUEENSLAND: Iron Range	EU364078	EU364486	EU364281
	Telicota argeus	92-ADW	AUSTRALIA: NSW: Hexhary	EU364081	EU364489	EU364284
	Cephrenes augiades	121-ADW	AUSTRALIA: NSW: Dudley	EU364079	EU364487	EU364282
	Sabera caesina	309-ADW	AUSTRALIA: N QUEENSLAND: Iron Range	EU364080	EU364488	EU364283
Gegenes Group	*Pelopidas mathias*	237-ADW	JAPAN: Saitama Pref.	EU364083	EU364491	EU364286
	Pelopidas thrax	570-ADW	GHANA: Ashanti Region DM02-086	EU364084	EU364492	EU364287
	Polytremis pellucida	234-ADW	JAPAN: Tokyo Pref.		EU364493	EU364288
	Polytremis pellucida	235-ADW	JAPAN: Saitama Pref.	EU364085		
	Iton watsonii	600-MCZ	THAILAND: Chiang Mai DL02P751	EU364082	EU364490	EU364285
MEGATHYMINAE						
Megathymini	*Megathymus streckeri*	36-ADW	USA: Colorado: Fremont Co.	EU364094	EU364504	EU364299
Agathymini	*Agathymus mariae*	587-ADW	USA: Texas: Val Verde Co.	EU364095	EU364505	EU364300

Full data are preserved with each voucher specimen and are available upon request.
Name combinations used in this list mostly follow Bridges (1993) and Mielke (2004, 2005).
Species-level names applied in this table that do not follow Bridges or Mielke are not indended to represent new taxonomic acts.
As shown by Hebert et al. (2004, also see Brower, 2006a), *Astraptes "fulgerator"* in Guanacaste, Costa Rica, apparently represents multiple species.
ADW = Collection of Andrew D. Warren, Castle Rock, Colorado, USA; vouchers will eventually be placed in a public institution.
AVZB = Collection of Andrew V. Z. Brower, Murfreesboro, Tennessee, USA; vouchers will eventually be placed in the AMNH, NY, USA.
MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.