Phylogeny of Moth Lacewings and Giant Lacewings (Neuroptera: Ithonidae, Polystoechotidae) Using DNA Sequence Data, Morphology, and Fossils

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ABSTRACT A phylogeny of lacewing families Ithonidae and Polystoechotidae is presented based on three gene markers (18S and 18S ribosomal DNA and CAD) and 23 morphological characters. Living and fossil genera presently placed in Polystoechotidae (Fontecilla Navás, Platystoechotes Carpenter and Polystoechotes Burmeister) and Ithonidae (Adamsiana Penny, Allorapisma† Makarkin & Archibald, Ithone Newman, Megalithone Riek, Oliarces Banks, Principiala† Makarkin & Menon, Rapisma Walker and Varnia Walker) were included in phylogenetic analyses (parsimony and Bayesian) and compared with outgroups selected from various families of Neuroptera. The resulting phylogeny recovered a monophyletic clade comprising Ithonidae and Polystoechotidae as hypothesized previously. Rapismatidae as a separate family is not supported and Ithonidae are rendered paraphyletic with three extant genera previously placed in Ithonidae (Adamsiana, Oliarces, and Rapisma), recovered deep within Polystoechotidae. The fossil genera Allorapisma† and Principiala† formed a sister-group relationship with Rapisma, also within Polystoechotidae. Due to the lack of mutually exclusive synapomorphies for either Ithonidae or Polystoechotidae, a single more inclusive family Ithonidae is proposed, including all ithonid genera and all genera previously placed in Polystoechotidae. Synapomorphies characterizing the revised concept of Ithonidae s.l. are discussed.

KEY WORDS phylogeny, Rapismatidae, Ithonidae, Polystoechotidae, lacewing

Ithonidae (moth lacewings) and Polystoechotidae (giant lacewings) are small families of robust and often hairy lacewings. Ithonidae presently comprises seven extant genera from Australia, Southeast Asia, and the New World, whereas Polystoechotidae comprise three extant genera from Australia, Southeast Asia, and the New World. Three genera of ithonids are found in Australia; Ithone Newman (Fig. 1A) contains 10 species, whereas Megalithone Riek and Varnia Walker contain two species each (Riek 1974). Three genera also are described from the New World, and all are monotypic, although additional undescribed species are known in collections (Oswald 1998b). Oliarces clara Banks (Fig. 1B) is known from arid areas of southwestern North America. Adamsiana curoi Penny is a montane species from Central America and is unique in that females are apertous, whereas males are macropterous (Penny 1996). Naradona mexicana Navás is only known from the original description and a hind wing figure of a single specimen from Mexico (Navás 1929a). A single ithonid genus is known from Southeast Asia (Rapisma McLachlan) containing ≈20 species from montane areas in Nepal to tropical lowlands in Thailand and Malaysia (Barnard 1981, Barnard and New 1985, New 1985, Yang 1993). Rapisma was previously considered as the sole genus in the family Rapismatidae, although there seems little evidence for maintaining this separation (Penny 1996, Makarkin and Menon 2007).

Polystoechotidae are represented by Platystoechotes Carpenter, Polystoechotes Burmeister (Fig. 1C), and Fontecilla Navás consisting of four species in total, Fontecilla graphicus Navás and Polystoechotes gazzullai Navás are known only from Chile, whereas Platystoechotes lineatus Carpenter is known from the southwestern United States (California) (Oswald 1998b). A second species of Polystoechotes (P. punctatus F.) is recorded from Canada south to Panama (Oswald 1998b, Archibald and Makarkin 2006; Fig. 1).

Specimens of both Ithonidae and Polystoechotidae are relatively rare in collections, although localized mass emergences have been recorded in Oliarces Banks and Ithone after seasonal rains (Riek 1974, Faulkner 1990). Larvae of Ithonidae and Polystoechotidae are known for Oliarces Banks, Megalithone, Ithone, Polystoechotes, and Platystoechotes (MacLeod 1964, Grebennikov 2004, Winterton et al. 2010). All are fossorial and in Ithonidae the mature larvae are scarabaeiform. Larvae of Ithonidae were originally re-
ported as predatory by Tillyard (1922), but Gallard (1932) subsequently proposed that they may be phytophagous or at least saprophagous on the bark of plant roots. This is yet to be confirmed, but obvious similarities in larval morphology between ithonids and polystoechotids suggest a common feeding biology. Ithonid larvae were recorded by Gallard (1932) to congregate around the bases of eucalyptus trees and observed “chafing,” shredding and actively feeding on the bark and roots to extract either sap or decaying liquid material. Similar congregational patterns have been recorded by Faulkner (1990) around the bases of creosote bushes (Larrea tridentata (DC) Coville] by Oliarces and around trees in montane regions by Polystoechotidae.

Based on detailed studies of larval head morphology, MacLeod (1964) proposed that Ithonidae and Polystoechotidae were sister-families closely related to Myrmeleontiformia (containing the families Ascalaphidae, Myrmeleontidae, Nemopteridae, Nymphidae, and Psychopidae). Phylogenetic studies using morphology, DNA sequence data, or a combination of the two have confirmed this hypothesis (Aspöck et al. 2001, Winterton 2003, Haring and Aspöck 2004, Winterton et al. 2010). The divergence time for the Ithonidae and Polystoechotidae clade is estimated as during the Late Triassic based on molecular data, with Ithonidae diverging from Polystoechotidae during the Jurassic (Winterton et al. 2010). Fossil Polystoechotidae are described from the Middle Jurassic to Late Eocene (Lambkin 1988, Ren et al. 2002, Makarkin and Archibald 2003, Archibald and Makarkin 2006), whereas “rapsimatid-like” fossil ithonids have recently been described from the Early Cretaceous and Early Eocene (Makarkin and Menon 2007, Makarkin and Archibald 2009).

The family-level placement of some ithonids has been questioned previously. Tillyard (1926) included Oliarces in Ithonidae that was supported by Carpenter (1951), but Lameere (1936) suggested that the genus belonged to Polystoechotidae. This was supported by a phylogenetic analysis using morphology and multiple molecular markers by Winterton et al. (2010), which strongly indicated that Oliarces should be trans-
Bayesian inference methods. Two extinct species of Ithonidae were undertaken using maximum parsimony and molecular DNA sequence data. Phylogenetic analyses of Polystoechotidae is presented based on morphology and molecular data for all extant genera of Polystoechotidae and Ithonidae, and a revised diagnosis and membership of the family. Recent collections of various genera of Ithonidae and Polystoechotidae to elucidate their phylogenetic placement. A phylogenetic study of these comparatively rare insects presented an opportunity to undertake a molecular phylogenetic analysis. Suitable for DNA sequencing, have preferred from Ithonidae to Polystoechotidae. Recent collections of various genera of Ithonidae and Polystoechotidae, suitable for DNA sequencing, have presented an opportunity to undertake a molecular phylogenetic study of these comparatively rare insects to try to elucidate their phylogenetic placement. A phylogeny for all extant genera of Polystoechotidae and Ithonidae is presented based on morphology and molecular DNA sequence data. Phylogenetic analyses were undertaken using maximum parsimony and Bayesian inference methods. Two extinct species of Ithonidae and Polystoechotidae are seen as separate families, or alternatively, united as a single family, is discussed. We conclude that the observed phylogeny better corresponds to the latter, and a revised diagnosis and membership of the family Ithonidae s.l. is proposed.

Materials and Methods

Terminology. Wing venation terminology used here generally follows Oswald (1993) and genital terminology follows Oswald (1998a).

Exemplar Selection. Ingroup taxa included all extant genera of Polystoechotidae (Polystoechotes, Platystoechotes, and Fontecilla) and Ithonidae (Adamsiana Penny, Ithona, Megalithone, oligarchs, Rapisma, and Varnia), except Narodona Navás as this genus is known only from a brief description and hind wing figure (Table 1; Fig. 2). Two relatively complete fossils of ithonids also were included (Principiala† and Alrorapisma†). Outgroups were included from lacewing families Osmylidae (Porismus striatus [Burmeister]), Nymphidae (Myiodactylus osmyloides [Brauer]), and Myrmeleontidae (Stilbopteryx costalis [Newman]). Twenty-three adult and larval characters were scored for all taxa, where data are available (Appendix 1). The two extant species represented by compression fossils could not be scored for all characters as some could not be observed.

Gene Sequencing. All gene sequences were downloaded from GenBank (Table 1) except Rapisma cryptunum New & Barnard. DNA sequencing for this additional taxon was carried out following the identical protocol outlined by Winterton et al. (2010). GenBank accession and specimen voucher numbers are presented in Table 1.

Sequence Alignment and Phylogenetic Analysis. Alignment of all sequences was done manually, although CAD was aligned with reference to translated amino acid sequences (standard eukaryote) by using MacClade, version 4.06 (Maddison and Maddison)
Parsimony analyses were conducted using PAUP*4.0b10 (Swofford 1999) using a branch and bound search protocol. Bootstrap support values for the parsimony analyses were calculated from 1,000 heuristic search (tree bisection and reconnection) pseudoreplicates of resampled data sets, each with 30 random additions (constant characters excluded).

Bayesian analyses were preformed using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The data were partitioned by data type (DNA sequence and

Fig. 2. Wings of Polystoechotidae and Ithonidae. (A) *Rapisma cryptum* New & Barnard. (B) *Oliarcés clara* Banks. (C) *Platystoechotes lineatus* Carpenter. (D) *Varnia implexa* (Navás). (E) *Ithone fulca* Tillyard. Scale = 2.0 mm. Abbreviations: 1A, 2A, 3A, first to third anal veins; CuA, anterior cubitus; CuP, posterior cubitus; MA and MP, anterior and posterior branches of media; phs, prehumeral space; R1, first branch of radius; Rs, radial sector; Sc, subcosta.
morphology), locus, and by the remaining two codon positions for each protein-coding locus. A separate GTR + \( \gamma \) nucleotide substitution model was applied to each DNA partition. The mk1 model (Lewis, 2001), with coding set to variable, was applied to the morphology partition. Each analysis consisted of four Markov chain Monte Carlo chains run simultaneously for 10 million generations. Trees were sampled every 1,000th generation. The first 1 million trees were discarded as burn-in. A majority rule consensus tree was computed with posterior probabilities (PP) for each node. Morphological characters were treated as unordered and equally weighted, with unknown states treated as ‘?’

Table 2. Character matrix for 23 morphological characters for three outgroup taxa (Porismus, Myiodactylus, and Stilbopteryx) and 11 ingroup taxa representing all extant, and two extinct, genera of Ithonidae and Polystoechotidae:

| Taxon          | Character 1 | Character 2 | Character 3 | Character 4 | Character 5 | Character 6 | Character 7 | Character 8 | Character 9 | Character 10 | Character 11 | Character 12 | Character 13 | Character 14 | Character 15 | Character 16 | Character 17 | Character 18 | Character 19 | Character 20 | Character 21 | Character 22 | Character 23 |
|---------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|

* Polymorphisms are indicated by a forward slash representing states 0 or 1.

Results

The combined sequence length for our concatenated molecular data set was 4479 bp (CAD = 2145 bp; 18S = 1848 bp; 16S = 486 bp) once ambiguously aligned sites (i.e., hypervariable stem regions in ribosomal genes) were removed. Addition of 23 morphological characters (Table 2) increased the combined data set to 452 characters. Average base frequencies across the data set for 16S were greatly A/T biased (A, 32.87%; C, 15.38%; G, 20.48%; and T, 31.26%; df = 39, P = 0.998), whereas for 18S sequences they were in relatively equal proportions except for a slightly lower cytosine content (A, 25.73%; C, 22.27%; G, 26.69%; T, 25.30%; df = 39, P = 1.000). Average base frequencies for CAD (all sites) were A, 32.57%; C, 15.38%; G, 20.48%; and T, 31.26% (df = 37, 0.002) and as is common with third positions, A/T bias was considerably greater (77.78%) than in either first (51.04%) or second (62.56%) codon positions. Average uncorrected sequence divergences across taxa for all DNA loci varied between the outgroup Porismus and most ingroup taxa at 13.9–15.5%, whereas between various ingroup genera, pairwise divergences ranged from 1.2% between closely related Ithone and Megalithone and 9.5% between the more distantly related Rapisma and Megalithone. Ithonidae were consistently divergent from Polystoechotidae by 7.5–10.9% (inclusive of Rapisma and Oliarces).

Inclusion of fossil exemplars in the analysis is likely to weaken the final estimate due to the low amount of data available (18 informative characters). Therefore initial parsimony and Bayesian analyses of the combined molecular and morphological data were undertaken with Allorapisma and Principiala excluded. The results of the Bayesian analysis are presented in Fig. 3; six most parsimonious trees were recovered from the parsimony analysis (tree length = 2106, consistency index [CI] = 0.708, retention index [RI] = 0.492), although the resolved parts of the topology were the same as the Bayesian tree. Two polytomies in the parsimony tree represented unresolved relationships among Adamsiana, Oliarces, and Rapisma as well as Ithone, Megalithone, and Varnia, respectively. All other branches on the tree were resolved with relatively high branch support. Adamsiana, Oliarces, and Rapisma were recovered as a clade deep within Polystoechotidae, subtended by a laddered grade consisting of Platystoechotes, Polystoechotes, and Fontecilla. Ithone, Megalithone, and Varnia formed a well supported clade sister to Polystoechotidae.

In a more inclusive analysis, all 14 taxa (including Allorapisma and Principiala) were compared in a combined molecular and morphological data analysis, consisting of 616 (18%) parsimony informative characters and 3,886 parsimony uninformative characters (including 3,395 constant characters). The parsimony analysis yielded three trees (length = 2,110 steps; CI = 0.707; RI = 0.494) of similar topology to the reduced taxon set phylogeny, with Allorapisma and Principiala placed a sister to the clade consisting of Adamsiana, Oliarces, and Rapisma. A Bayesian phylogram, with parsimony bootstrap values and Bayesian posterior probability values is presented in Fig. 4. In this analysis, the two fossil genera are placed as sister to Rapisma; otherwise, the tree topology is the same as the parsimony analysis. Lower posterior probability values on certain branches correspond to lower support or unresolved topologies in the parsimony tree. Adamsiana, Oliarces, and Rapisma are again placed deep within Polystoechotidae, with relatively high branch support. Ithonidae are again a well supported clade (88% bootstrap; 0.9 PP) represented by the extant Australian genera Megalithone, Ithone, and Varnia. Ithonidae + Polystoechotidae were recovered as a monophyletic clade with relatively strong branch support (73% bootstrap; 0.9 PP).

Morphological characters supporting the monophyly of the clade Ithonidae + Polystoechotidae include head retracted under prothorax (char. 1), humeral veinlet recurrent with multiple branches toward wing base (char. 2), and larval jaws short and broad for chafing (char. 23); characters one and 23 are apparently unique within the order and are a synapomorphy for Ithonidae + Polystoechotidae. As was found in Winterton et al. (2010), in all analyses Ithonidae was rendered paraphyletic with respect to Polystoechotidae with relatively high levels of sup-
port. Three genera presently placed in Ithonidae, i.e., *Adamsiana*, *Oliarces*, and *Rapisma*, were placed as a monophyletic clade deep within Polystoechotidae, although no discreet morphological characters could be found to support inclusion in this clade in the family. *Adamsiana*, *Rapisma*, and *Oliarces* are supported as a clade by wing trichosors being absent (char. 10) and pale wing venation (char. 11). When the fossil genera *Allorapisma* and *Principiala* were included in the analysis, they formed a sister-group relationship with *Rapisma*, although branch support within the clade comprising *Adamsiana*, *Rapisma*, *Oliarces*, *Allorapisma*, and *Principiala* became nonexistent. The sister-group relationship between *Allorapisma* and *Principiala* is supported by the divergent branching pattern of the forewing medial vein (char. 14) (Makarkin and Menon, 2007, Figs. 3 and 5; Makarkin and Archibald 2009, Figs. 2 and 3). The Australian genera of Ithonidae (*Ithone*, *Megalithone*, and *Varnia*) were recovered as a monophyletic clade in all analyses (bootstrap support = 88–99%; PP = 0.89–1.0) with *Megalithone* weakly supported as sister to *Varnia* in the pruned analysis. Five characters are synapomorphies for this clade: forewing with two radial branches originating on R (char. 13), mediuncus triangular (char. 19), male ectoprocts enlarged (homoplasious in *Oliarces*) (char. 20), male sternite 9 shovel-like (char. 21), and female sternite 9 forming a psammorotrum (char. 22).

**Discussion**

The results of this analysis using a combination of DNA sequence data and morphology support revised definitions and taxon composition for both Polystoechotidae and Ithonidae, although treating the clade as a single family should also be considered. Ithonidae, based on these results, comprises only the endemic Australian genera *Ithone*, *Megalithone*, and *Varnia*. Synapomorphies supporting Ithonidae in this context include forewing with two radial branches originating on R, mediuncus triangular, male sternite 9 shovel-like, and female sternite 9 forming a psammorotrum. Here, genera previously placed in Ithonidae, i.e., *Rapisma*, *Oliarces*, and *Adamsiana*, were recovered within Polystoechotidae along with *Polystoechotes*, *Platystoechotes*, and *Fontecilla*. Consequently, Polystoechotidae are predominantly distributed in the New World (five genera), with the single, relatively species-rich genus *Rapisma*, distributed throughout Southeast Asia. Multiple fossils of putative Polystoechotidae have been described, but definitive
Fig. 4. Phylogram of relationships of genera of Ithonidae and Polystoechotidae based on matching topologies from Bayesian and parsimony analyses of DNA sequence data and 23 morphological characters. Two additional extinct genera (Allorapisma† Makarkin & Archibald, Principiala† Makarkin & Menon) of Ithonidae also are included. Branch length represents number of changes. Bayesian Posterior Probability and bootstrap support values are presented in order on each branch. Wing drawings of Principiala† and Allorapisma† are modified after Makarkin and Menon (2007) and Makarkin and Archibald (2009), respectively.
family-level assignments have been problematic for some taxa (Lambkin 1988, Ren et al. 2002, Makarkin and Archibald 2003, Archibald and Makarkin 2006). The reason for this confusion is that synapomorphies defining Polystoechotidae are mostly lacking and characters used to differentiate the family are often plesiomorphies (Makarkin and Archibald 2003, Archibald and Makarkin 2006).

The placement of *Oliarcctidae* and *Rapismatidae* is not surprising with similarities between the two genera, and with Polystoechotidae, noted by previous authors. Lameere (1936) suggested that *Oliarcctidae* belonged to Polystoechotidae, and Grebennikov (2004) described a close morphological similarity of *Oliarcctidae* first instars to a putative polystoechodid. Makarkin and Archibald (2009) questioned the identity of this larva, suggesting that it could be an ithonid. Tillyard (1916, 1919b) suggested that *Rapismatidae* and *Oliarcctidae* do not belong in Ithonidae but require separate family status rather than placement in Polystoechodidae. Barnard (1981) supported the separation of Rapismatidae as a distinct family and listed eight characters that separated this family from Ithonidae. In his description and discussion of *Adamsiana*, Penny (1996) considered each of these characters in turn, with the new genus exhibiting character states of both Ithonidae and Rapismatidae and therefore suggested that the separation of the two families was not necessary. Neither Barnard (1981) nor Penny (1996) considered Polystoechodidae in their studies. Based on internal female genitalia morphology, Sziráki (1998) indicated that *Rapismatidae* showed a closer similarity with Polystoechodidae than Ithonidae. Our results are congruent with this conclusion, with *Rapismatidae* placed within Polystoechodidae and that the genus does not deserve separate family status.

The Mexican ithonid genus *Narodona* is known only from the original description and figure of the hind wing, with the type probably destroyed (Monserrat 1985). Based on the wing figure, this genus shows a clear affinity with *Adamsiana* (Penny 1996) and is most likely closely related. Given that *Adamsiana* is placed within Polystoechodidae in this analysis, it is clear that *Narodona* is probably a polystoechodid as well.

The incomplete yet highly autapomorphic wing venation of *Principia* and *Allorapismatidae* suggests placement within Polystoechodidae. The sister-group relationship with *Rapismatidae* supports previous suggestions by Makarkin and Menon (2007) of a close relationship among these genera based on overall similarities in wing venation and body shape.

Is there justification for maintaining two separate families, Ithonidae and Polystoechodidae? The sister-group relationship between Ithonidae and Polystoechodidae is supported by two morphological synapomorphies: head retracted under prothorax in adults and larval jaws very short and broad. Although larval biological data are incomplete for extant taxa (and nearly impossible for extinct taxa), it is likely that being fossorial, along with the probable phytophagous feeding biology, represent synapomorphies for this clade. Convincing mutually exclusive synapomorphies supporting both families are lacking, either as previously defined or based on our combined analyses. It seems that the most reasonable conclusion is to combine Ithonidae (including Rapismatidae) with Polystoechodidae as a single family containing all the genera presently included in these two families.

In conclusion, it is clear from the combined morphological and DNA sequence data presented here that the separation of Ithonidae and Polystoechodidae is not warranted. Our results strongly support either the transfer of *Adamsiana*, *Oliarcctidae*, and *Rapismatidae* to Polystoechodidae, or combining all the taxa into a single family. Morphological characters defining Polystoechodidae relative to Ithonidae are few, but there are some putative synapomorphies defining a single family, including adult and larval morphology and larval biology. Consequently, we have chosen the latter option as a more reasonable alternative to maintaining Ithonidae and Polystoechodidae as separate, but poorly defined, family groups. Further studies are required on the group, in particular, acquisition of DNA sequence data for *Narodona*, *Adamsiana*, and *Varnia* as well as biological studies of the larval morphology and feeding biology of all species.

**Family Ithonidae Newman, 1853, sensu novo**


Ithonidae: Tillyard, 1916: 274 [corrected name for Ithonesidae].


Rapismatidae Krüger, 1923: 72, 73.

Hapismatidae Navás, 1929b: 376 (as fam. nov.). Type genus: *Rapismatidae* [unjustified emendation of Rapismatidae].


**Diagnosis.** Robust, medium-sized to large neuropterans (forewing length, ~15–50 mm) distinguished from similar families by the presence of the following features: Head more or less retracted under pronotum; forewing elongate oval to subtriangular (broad-triangular in Brongnartiellidae, Osmylopsectyphonidae); antehumeral space long and broad in both wings, disproportionately large in genera with relatively narrow costal space; humeral veinlet well developed, recurrent, pectinate branched in both wings (in hindwing with at least one branch) (absent in hindwing of Hemerobiidae; absent in both wings of Dilaridae); apical area between C and R1, (or Sc+R1) markedly expanded (except perhaps Rapismatidae), with long, mainly forked veinlets of R1 or Sc+R1 in both wings (not markedly expanded in Hemerobiidae, Dilaridae); distal nygma present between two proximal branches of Rs in both wings (absent in Brongnartiellidae, Psy-
chopsidae, Hemerobiidae). Larval jaws relatively short and very broad basally; larva fossorial, associated with plant roots.


**Comments.** *Ithonidae* in a broader sense (i.e., inclusive of *Polystoechotidae* and *Rapismatidae*) as defined here includes six extinct and 10 extant genera restricted to Australia, the Oriental region and the New World. The family originated during the Triassic-Jurassic, more widely distributed during the Jurassic than the present (with many undescribed taxa from Chinese Jurassic deposits).

### Key to Extant Genera of *Ithonidae* s.l.

1. Wing venation pale green or white; wings rarely maculate ........................................ 2
   - Wing venation dark; wings usually strongly maculate or smoky infuscate ............. 4
2. Wing venation brilliant white; body dark (southwestern United States); *Oliarces* — Wing venation and body mostly pale (vivid green in live individuals) .................. 3
3. Wings usually spotted or banded; subcostal veinlets connected by numerous cross-veins so that serial ranks of cells present; female macropertoruous (Oriental region) ........................................ 4
   — Wings without infuscate patterning, membrane hyaline; subcostal veinlets not connected by cross-veins, single rank of cells; female apterous (New World) ....................... *Adamsiana*
4. Forewing R vein with additional branch, basal to pectinate Rs vein (Fig. 2E) (Australia) ....... 5
   — Forewing R vein with a single pectinate Rs vein (New World) ......................... 7
5. Wings mottled; cross-veins interlinking subcostal veinlets, creating multiple ranks of cells ............................................................. *Varnia*
   — Wings uniform infuscate; single row of cells in costal space ............................ 6
6. Fore basitarsus at most no longer than apical tarsomere; male ectoprocts enlarged and widened at apex ........................................ 7
   — Fore basitarsus much longer than apical tarsomere; male ectoprocts narrow and rounded at apex; wing uniform infuscate; single row of cells in costal space ................................. *Ithone*
7. Hind wing without prominent maculae (pterostigma slightly marked) .................... *Polystoechotes*
   - Hind wing with prominent maculae, particularly in posterior region ............... 9
8. Six to nine R1-Rs cross-veins in both wings (southwestern United States). .......... *Platystoechotes*
   — Less than three R1-Rs cross-veins in both wings (Chile) ................................. *Fontecilla*

### Appendix 1: Descriptions of Morphological Character States

1. **Head.** (0) clearly visible from above; (1) partially concealed beneath anterior margin of prothorax (Fig. 1). The derived state of this character is a synapomorphy for *Polystoechotidae* + *Ithonidae* and has been noted previously by Makarkin and Menon (2007).

2. **Forewing Humeral Veinlet.** (0) simple, cross-vein-like (Oswald 1998a: fig. 1); (1) recurrent, branched (Fig. 2B–E). The presence of the well-developed recurrent and branched humeral veinlet is characteristic of the order Neuroptera. It occurs in psychopoid-like families, *Ithonidae*, *Polystoechotidae*, *Hemerobiidae*, and some *Berothidae* and *Mantispidae*. In this analysis, the state is considered a synapomorphy of the genera of *Ithonidae* and *Polystoechotidae*; it has probably evolved independently at least three times, in *Hemerobiidae*, Psychopidae (and related fossil groups), and the clade *Berothidae* + *Mantispidae*.

3. **Proximity of Forewing Subcostal (Sc) and Radial (R) Veins.** (0) Sc and R1 completely separate distally (Fig. 2A and B, C, E); (1) closely approximated but not fused (Fig. 2C); (2) fused (Oswald, 1998a: fig. 1). Most of the ingroup exhibit the plesiomorphic state (0) with the Sc and R1 veins separate along entire length, whereas *Fontecilla*, *Polystoechotes*, and *Platystoechotes* have the veins closely approximated distally (1). Only the outgroups have Sc and R1 fused toward the apex of the wing (2). In the majority of the fossil species of *Polystoechotidae* not included in this analysis, however, these veins are fused.

4. **Number of Forewing Subcostal (Sc-R1) Cross-Veins.** (0) one, near wing base; (1) numerous cross-veins along length of subcostal area. The plesiomorphic state was most numerous, with the derived state present in *Porismus*, *Varnia*, *Rapisma*, *Allorapisma*†, and *Principiala*†.

5. **Number of Forewing Rs Branches.** (0) 4–8; (1) 9–12. Relatively few Rs branches is considered in this analysis as plesiomorphic and is found in *Porismus*, *Stilbopteryx*, and *Ithonidae*. The polarity of this character is not clear and in general, the states of character may depend largely on the wing size.

6. **Forewing Costal Space.** (0) relatively narrow basally and equal width along entire length (Fig. 2B); (1) distinctly dilated basally (Fig. 2C). In *Porismus*, the costal space is narrow basally and distinctly dilated at some distance from the base; state (0) is used in the analysis. This character is highly variable among all ingroup and outgroup taxa.

7. **Forewing Subcostal Veinlets.** (0) forked (Fig. 2A–E); (1) simple (Carpenter 1940: fig. 73). The forewing subcostal veinlets have extensive terminal
branching in all ingroup taxa; the amount of branching is much less in Myiodactylus.

8. Forewing Subcostal Veinlets. (0) not interconnected (Fig. 2B and E); (1) interconnected by cross-veins, forming multiple ranks of cells between costal margin and Sc (Fig. 2A and C, D). The derived state, with the subcostal veinlets interconnected and forming multiple ranks of cells is found in Principiala†, Allorapisma†, Varnia, Platystoechotes, and Rapisma. The genus Fontecilla possesses a few cross-veins, irregularity placed but not is serial ranks.

9. Forewing Gradate Series. (0) irregularly arranged, more than two series present (Fig. 2A and D, E); (1) two distinct series only (Fig. 2C). The derived state, with gradates arranged in two series is found only in Platystoechotes, Polystoechotes and Fontecilla.

10. Forewing Trichosors. (0) present along entire wing margin; (1) absent entirely, or present in only small portion of wing margin. The presence of wing trichosors is a synapomorphy for Neuroptera. The trichosors are frequently reduced in number or completely absent in many families, as found here in Stilbopteryx and the clade Adamsiana, Oliarces, Al-lorapisma†, and Rapisma.

11. Wing Venation. (0) dark (black or brown) (Fig. 2C-E); (1) pale (white to light green) (Fig. 2A and B). Pale wing venation is derived and is present in Myiodactylus and ingroup genera Oliarces, Rapisma, and Adamsiana. In Adamsiana, Myiodactylus, and Rapisma, the body and wings are green in living specimens, whereas in Oliarces the body is dark and wing veins are vivid white (Fig. 1B).

12. Forewing Shape. (0) symmetrical, largely ovoid (Fig. 2E); (1) asymmetrical tending toward falcate (Fig. 2C). An asymmetrical forewing is a synapomorphy for Polystoechotidae, although it is secondarily symmetrical in Oliarces, Allorapisma†, Principiala†, and some Rapisma.

13. Forewing Radial Branches. (0) single, pectinate Rs originating from R (Fig. 2A-C); (1) two branches originating from R, the distal branch being the pectinate Rs (Fig. 2D and E). The plesiomorphic condition occurs throughout Neuroptera. The derived condition represents a synapomorphy for Ithonidae s.s. (i.e., Ithone, Megalithone, and Varnia) and has evolved independently in Hemerobiidae and some Dilaridae and Kalligrammatidae. Carpenter (1951) incorrectly figured the wing of Ithone fusca Newman by omitting this basally free radial branch, instead showing only a single, pectinate Rs originating on R.

14. Fork of Forewing MP. (0) branches closely proximate, diverging acutely and only composed of two to three branches reaching wing margin (Fig. 2A-E); (1) branches widely divergent composed of more than five branches reaching wing margin (Makarkin and Menon 2007: figs. 3 and 5; Makarkin and Archibald 2009: figs. 2 and 3). The derived state is found only in the fossil genera Allorapisma† and Principiala†.

15. Hindwing Basal Cross-Vein r-m Shape. (0) sigmoid (Fig. 2E); (1) straight (Fig. 2B); (2) reduced or apparently absent (New 1983: fig. 2). The shape of the hindwing sigmoid vein was considered evidence for coalescence of MA with the radial vein in the forewing (e.g., Carpenter 1951), but now is interpreted as a cross-vein or “a cross-vein brace” (e.g., see Kukalová-Peck and Lawrence 2004: fig. 5). The sigmoid form (0) is plesiomorphic for Neuroptera and is exhibited by Megalithone, Ithone and Polystoechotes. Stilbopteryx, Principiala†, Adamsiana and Oliarces have a straight vein. In Porismus the vein is apparently absent or greatly reduced (New 1983), but it is sigmoid in other Osmylidae genera (e.g., Osmylus Latreille). Rapisma and Varnia show interspecific polymorphism in this character as the vein is present or absent between species.

16. Female Wings. (0) macropterous; (1) aupterus. The aupterus female is autapomorphic for Adamsiana (Penny 1996).

17. Tarsal Claw Shape. (0) narrow, without projections (Riek 1974: figs. 1 and 2); (1) relatively broad basally with small projection (Barnard 1981: fig. 7). The derived state of this character is autapomorphic for Rapisma (Penny 1996, Makarkin and Menon 2007).

18. Tibial Spurs. (0) present (Riek 1974: figs. 1 and 2); (1) absent. Tibial spurs are likely plesiomorphic throughout Neuroptera with numerous instances of secondary reduction, here exemplified by Myiodactylus and ingroup genera Adamsiana and Rapisma.

19. Male Genitalia, Mediuncus Shape. (0) as a lobed plate with ventral processes (Barnard 1981: figs. 12 and 15); (1) triangular (Acker 1960: figs. 58 and 60; as coxopodite 9); (2) reduced or absent (Penny 1996: figs. 4 and 5). Based on examinations of specimens of Oliarces in this study, it is clear that previous interpretations of the gonarcus being divided medially into two parts as illustrated by (Acker 1960: fig. 52) are incorrect, with only a single plate present. An interpretation of the gonarcus in Ithone as triangular is incorrect as well (Barnard 1981), as the darkly sclerotized mediuncus is triangular (1) in Ithone, Megalithone, and Varnia, with a weakly sclerotized and arched gonarcus present immediately dorsal of the mediuncus. The mediuncus is a medial, lobed, plate-like structure as the plesiomorphic state (0) in the outgroups, Rapisma, Fontecilla, Polystoechotes, and Platystoechotes, whereas it is weakly formed in Oliarces and Adamsiana (2).

20. Male Ectoprocts. (0) not enlarged (Penny 1996: fig. 3); (1) enlarged (Riek 1974: figs. 4 and 8). The male ectoprocts are enlarged in Ithone, Megalithone, Varnia, and Oliarces.

21. Male Sternite 9. (0) simple, not elongated (Barnard 1981: fig. 29); (1) elongated and shovel-like (Riek 1974: figs. 4 and 8). The derived state is exhibited by extant members of Ithonidae s. str. (i.e., Megalithone, Ithone, and Varnia). This character is not observable in the extinct species Principiala† and Allorapisma†.

22. Female Sternite 9 (= nine gonocoxites). (0) not enlarged (Barnard 1981: figs. 8 and 9); (1) enlarged (Riek 1974: figs. 6 and 41). The enlarged female sternite 9 of Megalithone, Varnia, and Ithone forms a psam-morotrum (Tillyard 1919a).
23. **Larval Jaw Shape.** (0) elongate and straight for piercing prey; (1) elongate, but curved for seizing prey; (2) relatively short, with very broad base (Grebennikov 2004: figs. 7 and 24, 31). Elongate and straight jaws modified for piercing (0) is plesiomorphic for Neuroptera (Winterton et al. 2010) and is found in *Porismus*; elongate and incurved apically jaws of *Myiodactylus* and *Stilbopteryx* are used for seizing prey (1). Larval stages known for *Ithone*, *Megalithone*, *Polystoechotes*, *Oliarces*, and *Platyptoechotes* and all exhibit the derived state of short jaws with a board base (2) (MacLeod 1964, Faulkner 1990, Grebennikov 2004, Winterton et al. 2010). This type of jaw is obviously not suitable for piercing or seizing prey but instead is used for scraping or chaffing the surface of plant roots, as observed in *Ithone* by Gallard (1932). All ingroup taxa were scored for this state. This type of specialized feeding biology and head morphology is a putative synapomorphy for the entire clade Ithonidae + Polystoechotidae.

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