

Phylogeny of the subfamilies of Ichneumonidae (Hymenoptera)

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Abstract

A combined morphological and molecular phylogenetic analysis was performed to evaluate the subfamily relationships of the parasitoid wasp family Ichneumonidae (Hymenoptera). Data were obtained by coding 135 morphological and 6 biological characters for 131 exemplar species of ichneumonids and 3 species of Braconidae (the latter as outgroups). The species of ichneumonids represent all of the 42 currently recognized subfamilies. In addition, molecular sequence data (cytochrome oxidase I “DNA barcoding” region, the D2 region of 28S rDNA and part of the F2 copy of elongation factor 1-alpha) were obtained from specimens of the same species that were coded for morphology (1309 base pairs total). The data were analyzed using parsimony and Bayesian analyses. The parsimony analysis using all data recovered previously recognized informal subfamily groupings (Pimpliformes, Ophioniformes, Ichneumoniformes), although the relationships of these three groups to each other differed from previous studies and some of the subfamily relationships within these groupings had not previously been suggested. Specifically, Ophioniformes was the sister group to (Ichneumoniformes + Pimpliformes), and Labeninae was placed near Ichneumoniformes, not as sister group to all Ichneumonidae except Xoridinae. The parsimony analysis using only morphological characters was poorly resolved and did not recover any of the three informal subfamily groupings and very few of the relationships were similar to the total-evidence parsimony analysis. The molecular-only parsimony analysis and both Bayesian analyses (total-evidence and molecular-only) recovered Pimpliformes, a restricted Ichneumoniformes grouping and many of the subfamily groupings recovered in

† Deceased.

the total-evidence parsimony analysis. A comparison and discussion of the results obtained by each phylogenetic method and different data sets is provided. It is concluded that the molecular characters produced results that were relatively consistent with traditional, non-phylogenetic concepts of relationships between the ichneumonid subfamilies, whereas the morphological characters did not (at least not by themselves). The inclusion of both molecular and morphological characters using parsimony produced a topology that was the closest to the traditional subfamily relationships. The method of analysis did not greatly affect the overall topology for the molecular-only analyses, but there were differences between Bayesian and parsimony results for the total-evidence analyses (especially near the root of the tree). The Bayesian results did not seem to be altered very much by the inclusion of morphological characters, unlike in the parsimony analysis. In summary, the following groups were supported in multiple analyses regardless of the characters used or method of tree-building: Pimpliformes, higher Ophioniformes, higher Pimpliformes, (Claseinae + Pedunculinae), (Banchinae + Stilbopinae), Campopleginae, Cremastinae, Diplazontinae, Ichneumoninae (including *Alomya*), Labeninae, Ophioninae, Poemeniinae, Rhyssinae, and Tersilochinae sensu stricto. Conversely, Ctenopelmatinae and Tryphoninae were never recovered without inclusion of other taxa. Based on the hypothesis of relationships obtained by the total-evidence parsimony analysis, the following formal taxonomic changes are proposed: Alomyinae Förster (= *Alomya* Panzer and *Megalomya* Uchida) is once again synonymized with Ichneumoninae and is now considered a tribe (Alomyini **rev. stat.**); and *Notostilbops* Townes is transferred from Stilbopinae to Banchinae, tribe Atrophini.

Keywords

Ichneumonidae, phylogeny, parsimony, Bayesian, classification, taxonomy

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Introduction

The catalogue of Yu et al. (2016) listed 25,285 described species of ichneumonids in 1601 genera. In terms of the subfamily classification within Ichneumonidae, there is general consensus for the taxonomic limits of most subfamilies; however, some authors disagree on a small minority (see Table 1). Townes (1969) established the modern subfamily classification recognizing 25 subfamilies. Morphological studies by several authors between 1969 and 2002 increased this number gradually to 37 (Wahl 1990, 1993; Gauld 1991; Porter 1998; Gauld et al. 2002a). The latter study recognized 37 subfamilies including the Pedunculinae, but not the Claseinae (both proposed by Porter 1998). Thus the total number recognized by morphology-based studies alone is 38 (see column 1 of Table 1).

From 1998–2009, several studies used single gene molecular evidence (the D2–D3 region of 28S ribosomal DNA) to examine ichneumonid subfamily relationships, either combined with morphological characters (Quicke et al. 2005; Quicke et al. 2009) or using molecular characters alone (Belshaw et al. 1998; Laurene et al. 2006). It was not until Quicke et al. (2005) that formal changes to the subfamily classification were proposed based on studies using molecular data. This study proposed two additional subfamilies: Nesomesochorinae and Nonninae for three genera previously included in Campopleginae. Further, Laurene et al. (2006) proposed the resurrection of Alomyinae (included in Ichneumoninae in previous classifications) (Wahl and Mason 1995). Subsequently, Quicke et al. (2009) evaluated sequences of 28S D2–D3 ribosomal DNA from 1001 species of Ichneumonidae and proposed the resurrection of one subfamily and the synonymy of three others (see column 2 of Table 1) (for a total of 39 subfamilies). The state of knowledge in ichneumonid systematics was summarized by Quicke (2015) and Broad et al. (2018).

More recently, Broad (2016) reversed one of the synonymies proposed by Quicke et al. (2009) by once again recognizing Neorhacodinae. Santos (2017), using both morphology and multi-gene sequence data, studied the relationships within Cryptinae

Table 1. Comparison of extant subfamilies of Ichneumonidae recognized by recent studies. Column 1: subfamilies recognized by morphological studies alone (up to 2002). Column 2: most recent analysis of all subfamily relationships using both morphological and molecular data. Column 3: subfamilies recognized following current study. *Brachyscleromatinae is now known as Sisyrostolinae (Bennett et al. 2013). Neorhacodinae was resurrected by Broad (2016) (considered part of Tersilochinae by Quicke et al. 2009). Ateleutinae and Phygadeuontinae were raised to subfamily status from within Cryptinae by Santos (2017).

Gauld et al. (2002a) + Porter (1998)	Quicke et al. (2009)	Current study (after formal changes)
Acaenitinae	Acaenitinae	Acaenitinae
Adelognathinae	Adelognathinae	Adelognathinae
Agriotypinae	Agriotypinae	Agriotypinae
	Alomyinae (previously part of Ichneumoninae)	
Anomaloninae	Anomaloninae	Anomaloninae
		Ateleutinae (previously part of Cryptinae)
Banchinae	Banchinae	Banchinae (including <i>Notostilbops</i>)
Brachycyrtinae	Brachycyrtinae	Brachycyrtinae
	Brachyscleromatinae* (previously part of Phrudinae)	
Campopleginae	Campopleginae	Campopleginae
Claseinae	Claseinae	Claseinae
Collyriinae	Collyriinae	Collyriinae
Cremastinae	Cremastinae	Cremastinae
Cryptinae	Cryptinae	Cryptinae
Ctenopelmatinae	Ctenopelmatinae	Ctenopelmatinae
Cylloceriinae	Cylloceriinae	Cylloceriinae
Diacritinae	Diacritinae	Diacritinae
Diplazontinae	Diplazontinae	Diplazontinae
Eucerotinae	Eucerotinae	Eucerotinae
Hybrizontinae (previously Paxylommatinae)	Hybrizontinae (previously Paxylommatinae)	Hybrizontinae
Ichneumoninae	Ichneumoninae	Ichneumoninae (including Alomyini)
Labeninae	Labeninae	Labeninae
Lycorininae	Lycorininae	Lycorininae
Mesochorinae	Mesochorinae	Mesochorinae
Metopiinae	Metopiinae	Metopiinae
Microleptinae	Microleptinae	Microleptinae
Neorhacodinae		Neorhacodinae
	Nesomesochorinae (including Nonninae of Quicke et al. (2005))	Nesomesochorinae
Ophioninae	Ophioninae	Ophioninae
Orthocentrinae	Orthocentrinae	Orthocentrinae
Orthopelmatinae	Orthopelmatinae	Orthopelmatinae
Oxytorinae	Oxytorinae	Oxytorinae
Pedunculinae	Pedunculinae	Pedunculinae
Phrudinae		Phygadeuontinae (previously part of Cryptinae)
Pimplinae	Pimplinae	Pimplinae
Poemeniinae	Poemeniinae	Poemeniinae
Rhyssinae	Rhyssinae	Rhyssinae
		Sisyrostolinae*
Stilbopinae	Stilbopinae	Stilbopinae (excluding <i>Notostilbops</i>)
Tatogastrinae	Tatogastrinae	Tatogastrinae
Tersilochinae	Tersilochinae (including Neorhacodinae + part of Phrudinae)	Tersilochinae
Tryphoninae	Tryphoninae	Tryphoninae
Xoridinae	Xoridinae	Xoridinae

and raised Phygadeuontinae (from the tribe Phygadeuontini) and Ateleutinae (from the tribe Cryptini, subtribe Ateleutina). In summary, 42 ichneumonid subfamilies were recognized prior to this study. Since Santos (2017), two other studies have been published which discuss ichneumonid subfamily relationships but neither of these proposed changes to the subfamily classification. Broad et al. (2018) provided an updated handbook to the ichneumonids of Britain and Ireland including discussion of all subfamilies, and Klopstein et al. (2019) used transcriptomes and target DNA enrichment to examine the relationships of Pimplinae and related subfamilies.

In terms of the relationships of the subfamilies, prior to about 1990, relationships could only be inferred by their relative arrangement in Henry Townes's *Genera of Ichneumonidae* (Townes 1969, 1970a, 1970b, 1971), a classification that was largely based on the supporting evidence (especially larval) in the character outline of Townes (1969) (pp. 29–35). As Townes (1969) wrote (p. 29): “Examination of the larval characters gave final proof of the basic faults in the old system and helped in the formulation of a new one”. Since 1990, phylogenetic hypotheses have been proposed for several groupings of subfamilies within Ichneumonidae. The informal name Pimpliformes was proposed for five subfamilies putatively related to Pimplinae (Wahl, 1990), and this group was further divided into eight subfamilies by Gauld (1991) through establishment of Diacritinae, Poemeniinae and Rhyssinae. Further, Wahl (1991) proposed the name Ophioniformes for eight subfamilies and Wahl (1993a) hypothesized that the two large subfamilies Cryptinae and Ichneumoninae were related and proposed the informal name Ichneumoniformes to comprise these two subfamilies along with Brachycyrtinae. The studies by Quicke and colleagues have for the most part, upheld these three groupings. Their studies also suggested placement for other subfamilies, for example, Quicke et al. (2009) placed an additional 8 subfamilies within the Ophioniformes (for a total of 16), 3 additional subfamilies in Ichneumoniformes (for a total of 5), and 1 additional subfamily (Collyriinae) in Pimpliformes (for a total of 9). Still, the study of Quicke et al. (2009) had two subfamilies with uncertain affinity (Eucerotinae and Microleptinae). Their study included the most comprehensive taxon sampling of any phylogenetic study of Ichneumonidae, including species from all subfamilies, but the analysis included only one gene and morphology was coded mostly at the subfamily and tribal levels (88 terminal taxa). More recent studies (Santos 2017 which sampled heavily within Ichneumoniformes and Klopstein et al. 2019 that focused on Pimpliformes) included much more molecular data, but with a more limited taxonomic scope. The overall purpose of this study is to examine the relationships of the subfamilies of Ichneumonidae based on phylogenetic analyses using both morphological and molecular sequence data. The study is of interest because it includes the largest morphological data set for Ichneumonidae that has been coded for individual exemplar species. Novel morphological characters are introduced, especially for larvae, and the nuclear gene elongation factor 1-alpha is sequenced across the entire family for the first time. The results will be compared to previous hypotheses of relationships (e.g., Wahl and Gauld 1998, Quicke et al. 2009, Santos 2017, Klopstein et al. 2019) and will provide another hypothesis of relationships against which future studies can be compared.

For the purposes of this study, the following definitions for the subfamily groupings are used:

- 1) Ophioniformes includes the following 18 subfamilies: Anomaloninae, Banchinae, Campopleginae, Cremastinae, Ctenopelmatinae, Hybrizontinae, Lycorininae, Mesochorinae, Metopiinae, Oxytorinae, Neorhacodinae, Nesomesochorinae, Ophioninae, Sisyrostolinae, Stilbopinae, Tatogastrinae, Tersilochinae and Tryphoninae. This concept is the same as that of Quicke et al. (2009)—the 16 subfamilies listed under Ophioniformes in their table 4 plus Neorhacodinae resurrected by Broad (2016) and Tatogastrinae which was presumably accidentally omitted from their table. Note that this group includes the eight subfamilies included by Wahl (1991) when the name was proposed. Gauld et al. (1997) included nine subfamilies: the eight of Wahl (1991) and Tersilochinae. Gauld et al. (1997) also coined the name Tryphoniformes to comprise Adelognathinae, Eucerotinae, Tryphoninae and Townesioninae (the latter now synonymized with Banchinae). Adelognathinae and Eucerotinae are now believed more closely related to Ichneumoniformes (Quicke et al. 2009, Santos 2017) and Tryphoninae is thought to belong to Ophioniformes (Quicke et al. 2009), as sister group to all other subfamilies, therefore we do not use the term Tryphoniformes. Within Ophioniformes is a group of closely related subfamilies that Quicke et al. (2009) called the “higher Ophioniformes” which we define as Anomaloninae, Campopleginae, Cremastinae, Nesomesochorinae and Ophioninae.
- 2) Pimpliformes includes the following nine subfamilies: Acaenitinae, Cylloceriinae, Diacritinae, Diplazontinae, Orthocentrinae, Pimplinae, Poemeniinae, Rhyssinae and in addition, Collyriinae. This definition corresponds to the concept of Quicke et al. (2009), which was the same as Wahl and Gauld (1998), except for the inclusion of Collyriinae in Quicke et al. (2009). The higher Pimpliformes is comprised of Pimplinae, Poemeniinae and Rhyssinae (Quicke et al. 2009). Note that the term “higher Pimpliformes” was used previously by Gauld (1991) for a group comprised of Diplazontinae, Orthocentrinae and Microleptinae, but this is not the definition used in the current study. Gauld (1991) believed that Rhyssinae was sister subfamily to all others in Pimpliformes, followed by a polytomy of Pimplinae, Poemeniinae and Acaenitinae leading to the koinobiont, endoparasitoid fly parasitoids (Cylloceriinae and his “higher Pimpliformes”). The sister group relationship of Rhyssinae to the rest of Pimpliformes was not upheld by the studies of Wahl and Gauld (1998) and Quicke et al. (2009), but the grouping of Rhyssinae, Poemeniinae and Pimplinae was strongly supported in both studies.
- 3) Ichneumoniformes is considered in two senses: a) in the strict sense (Ichneumoniformes sensu stricto) as originally proposed by Wahl (1993a) and including only Brachycyrtinae, Cryptinae (including Ateleutinae and Phygadeuontinae) and Ichneumoninae (including Alomyinae), and b) in the broad sense (Ichneumoniformes sensu lato) comprised of Ichneumoniformes s.s. plus seven related subfamilies which will be further described and discussed in the Results and discussion section.

In addition, Quicke et al. (2009) defined the following higher groups:

- 4) Xoridiformes comprised of Xoridinae
- 5) Labeniformes comprised of Labeninae
- 6) Orthopelmatiformes comprised of Orthopelmatinae
- 7) Brachycyrtiformes comprised of Brachycyrtinae, Claseinae and Pedunculinae.

See the Results section on Support/ relationships of subfamilies (below) for discussion on the support/ placement of these groups in the current study.

Methods

Outgroups

There is very strong evidence that Braconidae is the sister group of Ichneumonidae based on morphology (Rasnitsyn 1988; Sharkey and Wahl 1992) as well as combined morphological and molecular evidence (Heraty et al. 2011; Sharkey et al. 2012; Peters et al. 2017; Branstetter et al. 2017). The three exemplar species (from three subfamilies) chosen for this study were species used in the studies of Heraty et al. (2011) and Sharkey et al. (2012) which was done to aid comparison between these studies and to ensure inclusion of a range of life strategies in our outgroups: *Doryctes erythromelas* (Brullé) (Doryctinae) (idiobiont ectoparasitoid); *Aleiodes terminalis* Cresson (Rogadinae) (koinobiont endoparasitoid) and *Rhysipolis* sp. (Rhysipolinae) (koinobiont ectoparasitoid).

Ingroup

Ingroup taxa were chosen in order to provide complete coverage of all currently recognized subfamilies based on the most recent study of ichneumonid relationships (Quicke et al. 2009) as well as to try to include the widest range of morphological variation among the species in each subfamily. In addition, some equivocally placed taxa were deliberately included (see Results and Discussion). Apart from taxonomic coverage and choosing species to maximize morphological divergence within subfamilies, the following additional criteria were used for choosing ingroup exemplar taxa (in order of importance): a) availability of fresh specimens from which all three DNA regions could be obtained; b) knowledge of the larva; c) knowledge of biological (life-history) traits; d) knowledge of the egg. All taxa used in this study are listed in the morphological character matrix (Table 2) as well as the list of taxa examined (Appendix 2).

Voucher specimens and larval slides are deposited at the Australian National Insect Collection, Canberra, Australia (ANIC) (J. Rodriguez), the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (CNC) (A. Bennett), the

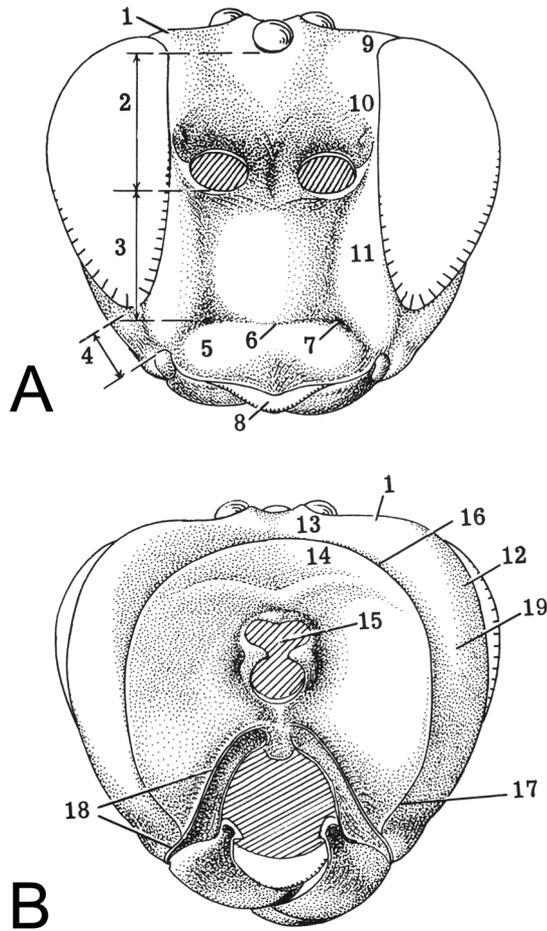
Entomology collection, Department of Biology, Utah State University, Logan, Utah, USA (EMUS) (D. Wahl), the Smithsonian Institute, Washington, DC (NMNH) (R. Kula) and the University of Kentucky, Lexington, Kentucky, USA (UKY) (E. Chapman).

Morphological character coding

We used a species exemplar approach in this study, rather than coding morphological characters at the tribal or subfamily level as has been done in other studies on family and subfamily relationships within Hymenoptera (Brothers and Carpenter 1993 for Aculeata; Quicke and van Achterberg 1990 for Braconidae; Quicke et al. 2009 for Ichneumonidae). Whereas the species exemplar approach is very time-consuming for large datasets, it is preferable (if possible) in order to make the character coding as objective and reproducible as possible. It also permits testing of the monophyly of the subfamilies and tribes (evidence of monophyly is provided when all constituent taxa cluster together). For a comparison of the exemplar and generic abstraction approaches, see Gauld et al. (2002b), which included both types of coding for Pimplinae. In all cases, coding of adult morphology was done with reference to the actual specimen from which DNA was obtained, as well as other authoritatively identified, conspecific specimens used to ensure that the DNA voucher was representative of the species. Larval characters were coded directly from conspecific larval slides of our exemplar species (when known), or if the larva of our exemplar species was not known, coding was done with reference to slides and or literature figures of species within the same genus. In cases in which there was no larval knowledge of any species within the genus, the larval characters were coded as missing. The same strategy was used for the egg and biological characters.

Morphological terms, measurements and photography

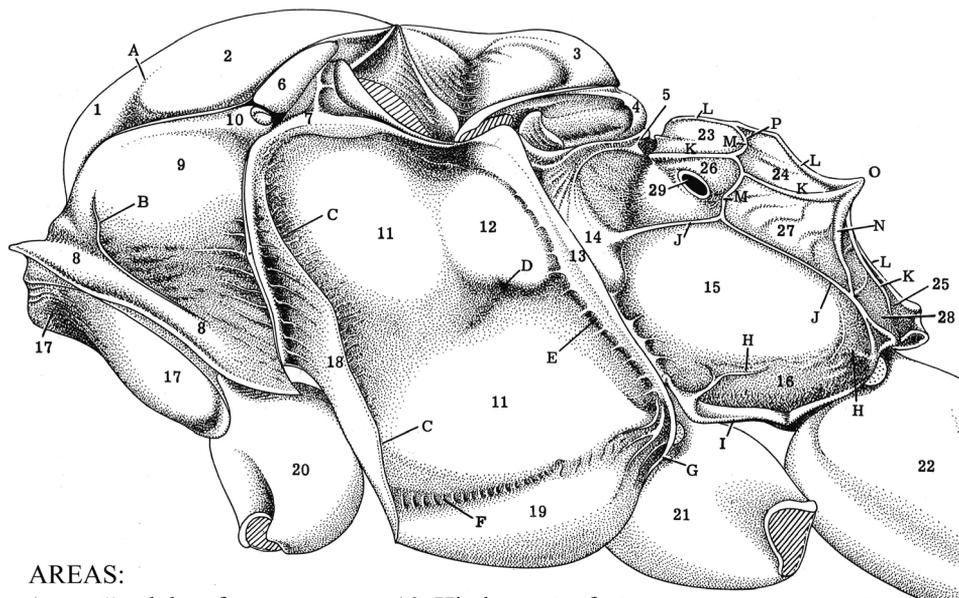
All terms of ichneumonid morphology follow Townes (1969) with the following modifications: hypostomal carina (Fig. 1, structure #18) for 'oral carina', supra-antennal area (Fig. 1, structure #2) for 'frons', supraclypeal area (Fig. 1, structure #3) for 'face', gena (Fig. 1, structure #19) for 'temple', occiput (Fig. 1, structure #14) for 'postocciput', malar space (Fig. 1, structure #4) for 'cheek', epicnemial carina (Fig. 2C) for 'prepectal carina', laterotergites (Fig. 79) for 'epipleura', gonoforceps (Fig. 92) for 'claspers', and hypopygium (Fig. 86) for 'subgenital plate'. The term 'mesosoma' is used for the body region that includes the thorax and first abdominal segment (the propodeum). The term 'metasoma' is used for the apparent abdomen, with MS1, MS2, etc. referring to metasomal segments 1, 2, etc., T1, T2, etc. referring to the corresponding tergites; L1 and L2, etc. referring to the laterotergites and S1, S2, etc. referring to the sternites. The term T2+ refers to tergite 2 and all tergites posterior to T2. Terms of relative position of the body follow Goulet and Huber (1993). Wing venation terms follow the Comstock-Needham system as updated by Ross (1936) and incorporate



- | | |
|---|---|
| 1, 13. Vertex | 9, 10, 11. Paraocular area |
| 2. Supra-antennal area | 12. Genal orbit |
| 3. Supraclypeal area | 14. Occiput |
| 4. Malar space (= cheek) | 15. Foramen magnum |
| 5. Clypeus | 16, 17. Occipital carina
(17 = genal carina) |
| 6. Epistomal suture | 18. Hypostomal carina (= oral carina) |
| 7. Anterior tentorial pit (= clypeal fovea) | 19. Gena |
| 8. Labrum | |

Figure 1. Head of an ichneumonid. **A** anterior view **B** posterior view (modified from Townes 1969).

the recommendations of Goulet and Huber (1993) except for naming of the vein that forms the distal edge of fore wing cell $I+2Rs$ (the 'areolet' of Townes 1969). This vein is of uncertain origin and is here referred to as 'vein $3rs-m$ ' (Fig. 4A) in conformity with Wahl and Gauld (1998) (= $3r-m$ vein of Sharkey and Wahl 1992). The following terms for specialized structures are defined: epomia (Fig. 2b): a raised ridge (carina) on the pronotum (Figs 30–31); glymma (Fig. 5, structure #11): the lateral depression



AREAS:

- | | | |
|---------------------------------------|-----------------------------------|------------------------------|
| 1. Median lobe of mesoscutum | 10. Hind corner of pronotum | 18. Epicnecium (= prepectus) |
| 2. Lateral lobe of mesoscutum | 11, 12, 18. Mesopleuron | 19. Mesothoracic venter |
| 1, 2. Mesoscutum | [mesepisternum] | 20. Fore coxa |
| 3. Scutellum | 12. Hypoepimeron (= speculum) | 21. Middle coxa |
| 4. Metanotum (= postscutellum) | 13. Mesepimeron | 22. Hind coxa |
| 5. Hind margin of metanotum | 14. Upper division of metapleuron | 23-28. Propodeum |
| 6. Tegula | 15. Lower division of metapleuron | 23. First lateral area |
| 7. Subalar ridge (= subtegular ridge) | 16. Juxtacoxal area | 24. Second lateral area |
| 8. Collar | 17. Propleuron | 25. Third lateral area |
| 8, 9, 10. Pronotum | | 26. First pleural area |
| | | 27. Second pleural area |
| | | 28. Third pleural area |
| | | 29. Propodeal spiracle |

CARINAE AND GROOVES:

- | | |
|---|--|
| A. Notaulus | I. Submetapleural carina |
| B. Epomia | J. Pleural carina |
| C. Epicnemial carina (= prepectal carina) | K. Lateral longitudinal carina of propodeum |
| D. Scrobe (= mesopleural fovea) | L. Median longitudinal carina of propodeum |
| E. Mesopleural groove | M. Anterior transverse carina of propodeum (= basal transverse carina) |
| F. Sternaulus | N. Posterior transverse carina of propodeum (= apical transverse carina) |
| G. Posterior transverse carina of mesothoracic venter | O. Propodeal apophysis or crest |
| H. Juxtacoxal carina | P. Costula [part of anterior transverse carina] |

Figure 2. Mesosoma of an ichneumonid, lateral view (modified from Townes 1969).

sub-basally on T1; notaulus (Fig. 3A): a longitudinal groove sublaterally on the mesoscutum; sternaulus (Fig. 2F): a longitudinal groove subventrally on the mesopleuron (not to be confused with the mesopleural groove which is more dorsal (see Fig. 30).

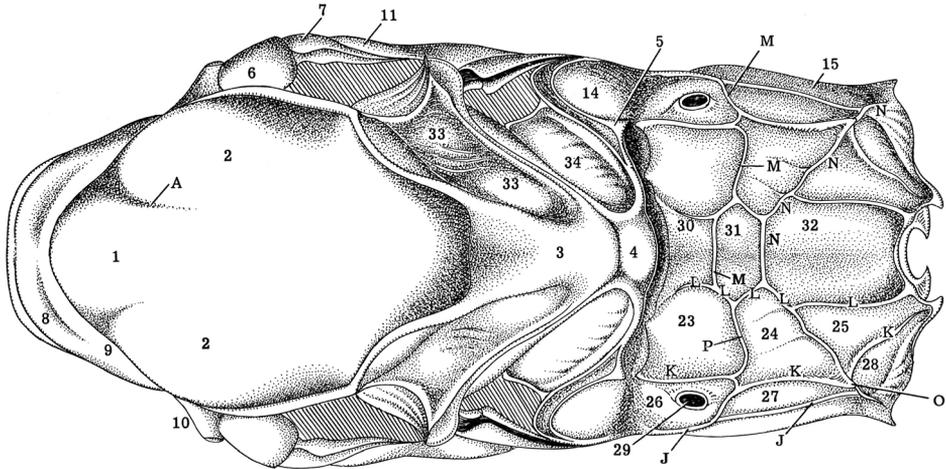
The carinae on the propodeum (see Figs 3, 4) can present difficulties for scoring of their presence and absence, depending on interpretation of their homology. For example, if only one transverse carina is present near the longitudinal middle of the propodeum, there is ambiguity with respect to whether this should be considered the anterior or posterior transverse carina. To help make scoring of the propodeal carinae more objective, the following conventions were used:

- 1) In cases in which there is ambiguity between the anterior and posterior transverse carinae, the posterior transverse carina was given precedence.
- 2) In cases in which there is ambiguity between the medial and lateral longitudinal carinae, the medial longitudinal carinae were given precedence.
- 3) In cases in which longitudinal and transverse carinae run obliquely together across the propodeum, the transverse carina was given precedence over the longitudinal carinae.
- 4) In cases in which an abscissa of a carina is incomplete (e.g., the costula of many specimens of Campopleginae), the abscissa was considered present if it extended half the way across the area in which it is located or greater, or if this could not be determined (e.g., no other carinae are present on the propodeum), one sixth of the length (for longitudinal carinae) or width (for transverse carinae) of the propodeum.

Digital photos at the CNC were taken using a Leica MZ16 stereomicroscope with motorized focus drive attached to a Leica DFC420 digital camera. Photos were combined and edited using Leica Application Suites Montage Multifocus software V3.8, Auto-Montage Pro 5.01 and Adobe Photoshop CS4. Photos taken at EMUS were taken with an EntoVision micro-imaging system. This system consists of a Leica M16 zoom lens attached to a JVC KY-75U 3-CCD digital video camera that feeds image data to a desktop computer. The program Archimed 5.3.1 was used to merge an image series (representing typically 15–30 focal planes) into a single in-focus image. Lighting was provided by an EntoVision dome light.

Molecular protocols

Most sequences in this study were obtained by sequencing specimens at the Canadian National Collection of Insects, Arachnids and Nematodes (CNCI), except as noted in Appendix 2 (11 sequences downloaded from Genbank: the nine outgroup sequences and 28s DS for *Poecilocryptus nigromaculatus* Cameron and *Hellwigia obscura* Gravenhorst). GenBank accession numbers are listed in Appendix 2. All sequences, including those downloaded from GenBank, were compared to published sequences of putatively related taxa to verify sequence veracity using the nucleotide BLAST tool (Altschul et al. 1990) through GenBank (Benson et al. 2017).



AREAS:

- | | | |
|---------------------------------------|-----------------------------------|----------------------------------|
| 1. Median lobe of mesoscutum | 8, 9, 10. Pronotum | 26. First pleural area |
| 2. Lateral lobe of mesoscutum | 10. Hind corner of pronotum | 27. Second pleural area |
| 1, 2. Mesoscutum | 11. Mesopleuron | 28. Third pleural area |
| 3. Scutellum | [mesepisternum] | 29. Propodeal spiracle |
| 4. Postscutellum | 14. Upper division of metapleuron | 30. Basal area |
| 5. Hind margin of metanotum | 15. Lower division of metapleuron | 31. Areola |
| 6. Tegula | 23–32. Propodeum | 32. Petiolar area |
| 7. Subalar ridge (= subtegular ridge) | 23. First lateral area | 33. Axillary trough of mesonotum |
| 8. Collar | 24. Second lateral area | 34. Axillary trough of metanotum |
| | 25. Third lateral area | |

CARINAE AND GROOVES:

- | | |
|---|--|
| A. Notaulus | I. Submetapleural carina |
| B. Epomia | J. Pleural carina |
| C. Epicnemial carina (= prepectal carina) | K. Lateral longitudinal carina of propodeum |
| D. Scrobe (= mesopleural fovea) | L. Median longitudinal carina of propodeum |
| E. Mesopleural groove | M. Anterior transverse carina of propodeum (= basal transverse carina) |
| F. Sternaulus | N. Posterior transverse carina of propodeum (= apical transverse carina) |
| G. Posterior transverse carina of mesothoracic venter | O. Propodeal apophysis or crest |
| H. Juxtacoxal carina | P. Costula [part of anterior transverse carina] |

Figure 3. Mesosoma of an ichneumonid, dorsal view (modified from Townes 1969).

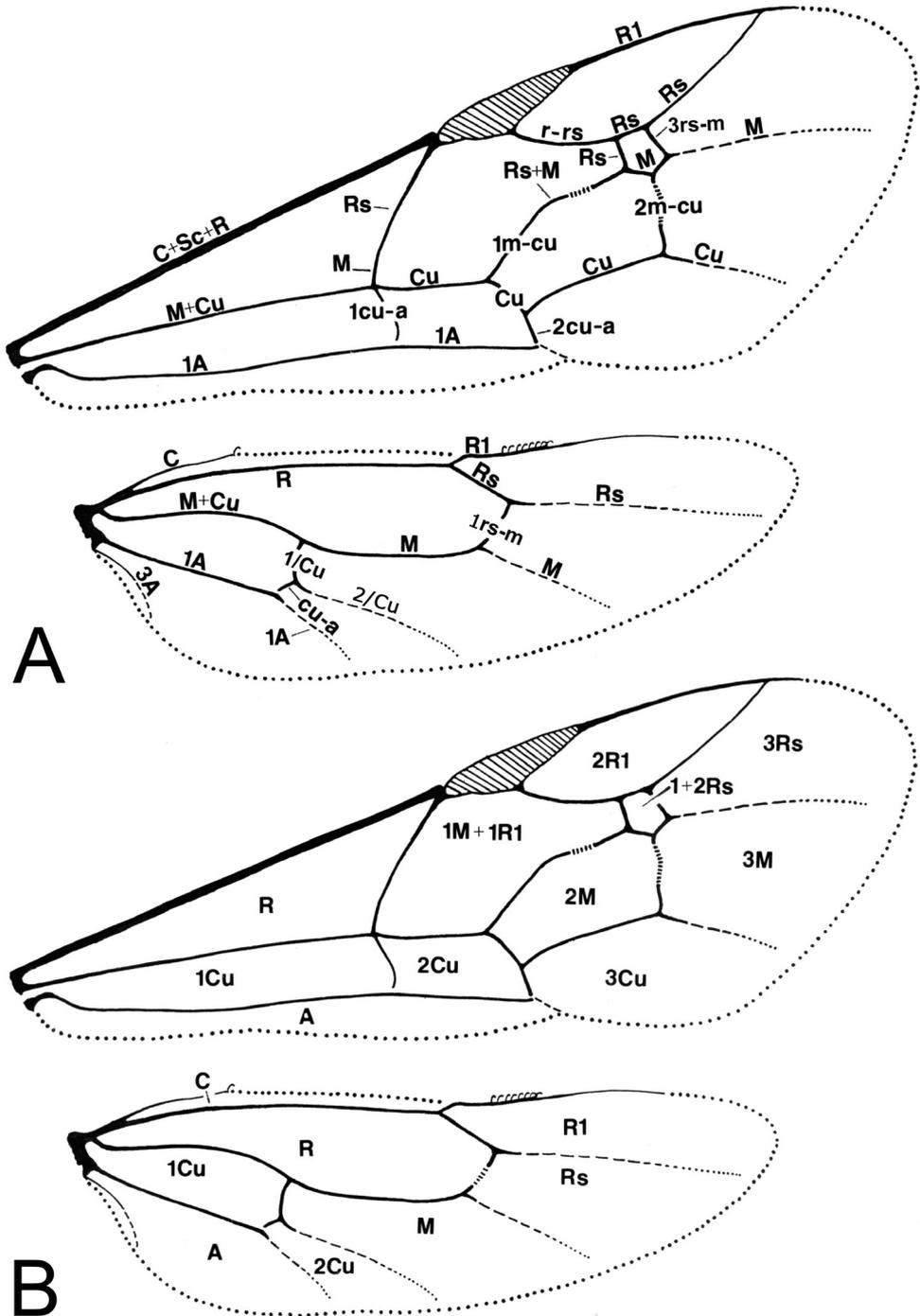
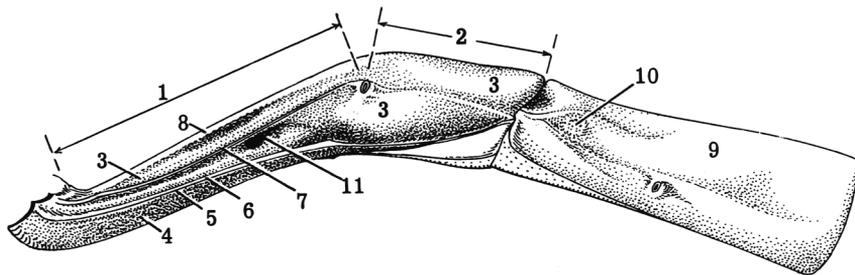


Figure 4. Fore and hind wings of an ichneumonid (Ross system). **A** wing veins **B** wing cells (modified from Townes 1969).



- | | |
|-------------------------|-------------------------|
| 1. Petiole | 7. Dorsolateral carina |
| 2. Postpetiole | 8. Median dorsal carina |
| 3. Tergite 1 | 9. Tergite 2 |
| 4. Sternite 1 | 10. Thyridium |
| 5. Tergosternal suture | 11. Glymma |
| 6. Ventrolateral carina | |

Figure 5. First and second metasomal tergites of an ichneumonid, lateral view (modified from Townes 1969).

Molecular extracts were obtained using standard protocols outlined in DNeasy Blood and Tissue extraction kit instructions (Qiagen, Gaithersburg, MD, USA). A single mid leg was macerated except for small specimens in which a hind and mid leg were used. PCRs were carried out using 50 μ l reactions containing 4 μ l DNA extract, 1 μ l of each primer, 5 μ l PCR buffer, 1 μ l DNTPs, 1 μ l $MgCl_2$, 0.25 μ l Taq and 36.75 μ l RNase-free water. Primers were as follows: Cytochrome oxidase I (COI) (F) (LCO1490): GGTCAACAAATCATAA AGATATTGG; (R) (HCO2198): TAAACTTCAGGGTGACCAAAAAATCA (Folmer et al. 1994); 28S (F) (3665): AGAGAGAGT TCAAGAGTACGTG; (R) (4068): TTGGTCCGTGTT TCAAGACGGG (Belshaw et al. 1998); F2 copy of elongation factor 1-alpha (EF1a) (F): AGATGGGYAAR GGTTCCTTCAA; (R): AACATGTTGTDCCGTGCCATCC (Belshaw and Quicke 1997). Verification that only the F2 copy was present was done by comparing our sequences to published F1 and F2 sequences from Klopstein and Ronquist (2013). PCR protocols followed the studies listed above for each molecule. The PCR products were purified using the QIAquick PCR Purification Kit Protocol (Qiagen). Problems with PCR amplification of EF1a resulting from multiple gene copies were resolved through gel-cutting. All centrifugation steps were performed for 60 s and samples were left to incubate for two minutes in Buffer PE (to reduce salt concentration), and five minutes in Buffer EB. Sequencing reactions were performed in a total reaction volume of 10 μ l, with 1 μ l ddH₂O, 3 μ l of sequencing buffer, 1 μ l of primer with concentrations ranging from 51.8 to 69.9 nmol, 1 μ l of BigDye Terminator (PE Applied Biosystems, Foster City, CA, USA), and 4 μ l of purified PCR product. Sequencing was performed in both directions at the Agriculture & Agri-Food Canada, Eastern Cereal and Oilseed Research Centre Core Sequencing Facility (Ottawa, ON, Canada) on an Applied Biosystems Incorporated PRISM 3100-Avant Genetic Analyzer.

Sequence alignment

Preliminary alignment of coding genes (COI and EF1-a) was done using ClustalW (Thompson et al. 1994) followed by alignment with reference to amino acid coding using MacClade 4.0 (Maddison and Maddison 2001) and Mesquite 2.75 (Maddison and Maddison 2011). For COI, third codon positions were excluded from analysis because of saturation. Alignment of 28S used the secondary structure model for Ichneumonoidea (Gillespie et al. 2005). The following invariant or unalignable regions were excluded from analyses: NHR(1), REC(1'), RAA(2), RAA(3), NHR(2), REC(2'), RAA(7), REC(3'), RAA(8), REC(4), REC(5), REC(6), RAA(10), REC(5'), RAA(15). The number of aligned bases were as follows: COI: 441; 28s D2: 448; EF1a: 417.

Aligned sequences are available in Suppl. materials 1–4 and by request from the corresponding author.

Phylogenetic analyses

Parsimony analysis was performed using TNT v. 1.1 (Goloboff et al. 2003). All characters were treated as unordered and equally weighted in order to avoid placing subjective, pre-conceived notions on the direction and relative importance of particular transitions. The optimal score was found 20 times using the default settings of “xmult” plus 10 cycles of tree-drifting. Optimal trees found were then imported into Winclada 1.00.08 (Nixon 2002) for tree-viewing and were then exported to NONA 2.0 (Goloboff 1999) for additional branch-swapping using the command “max” to find the complete set of equally parsimonious cladograms for the starting cladograms. NONA did find additional trees and this step is highly recommended when doing parsimony searches with TNT. Strict consensus cladograms were produced using WinClada. The taxonomy depicted in all cladograms (Figs 117–124) represents classification prior to this study. Taxa for which formal nomenclatural changes are made are indicated with an asterisk (see text of respective taxa for details). Cladograms showing optimization of individual characters (Figs 122–124) were produced using MacClade 4.03 (Maddison and Maddison 2001) and Mesquite 2.75 (Maddison and Maddison 2011). Nodal support on parsimony cladograms is shown by optimization of morphological characters using ACCTRAN which favours reversals over parallelisms as well as by decay index values (Bremer 1994) calculated using TNT (shown as a boxed number under each node or taxon) (see Fig. 117). Parsimony analyses were run for the total-evidence data set (Fig. 117), morphological characters only (Fig. 118) and sequence data only (Fig. 119).

Bayesian analyses were conducted using MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). Model testing was done in JModelTest 0.1.1 (Posada 2008) with the best-fitting models for each partition as follows: COI (TIM+I+G); 28S (GTR+F); EF1a (K80+I+T), morphology (discrete model with gamma). Bayesian analysis was run with all parameters unlinked across partitions. In addition for 28S, secondary structure stems versus loops were analyzed using separate models. Eight independent runs

of 4 chains each were run for 10 million generations, with trees sampled every 1000 generations. Chains were run until the average standard deviation of split frequencies went below 0.01. For each analysis, the trees in a burn-in period were excluded, and the remaining post-burn-in trees were used to construct a maximum clade credibility tree. Nodal support is indicated using Bayesian Posterior Probabilities (BPP) shown to the right of each node. Bayesian analyses were run for the total-evidence data set (Fig. 120) and sequence data only (Fig. 121). Trees from Bayesian analyses were made using FigTree 1.4.3 (Rambaut 2016).

Results and discussion

Morphological characters (see Table 2 for matrix)

In total, 141 morphological and biological characters were included in the analyses: 104 adult, 28 larval, 3 egg and 5 biological.

1. Clypeus: 0) comprised of one part (Fig. 1); 1) differentiated into basal and apical parts (Fig. 8).
2. Clypeus and supraclypeal area: 0) separated by groove or indentation (Fig. 1); 1) without any impression separating them – more or less flat or uniformly convex (Fig. 9).
3. Clypeal margin in anterior view: 0) simple, truncate to slightly convex or slightly concave (Fig. 12); 1) medially with apical denticle or denticles (not bilobed) (Fig. 10); 2) apically bilobed (strongly concave medially) (median denticle may be present or absent) (Fig. 11).
4. Clypeal margin vestiture: 0) with small scattered setae or lacking setae; 1) with regularly spaced strong setae (Fig. 12).
5. Mandibles: 0) bidentate, gradually to strongly tapering (Fig. 1); 1) unidentate, chisel shaped (Fig. 13); 2) unidentate, wide apically and twisted (Fig. 14); 3) reduced to flap (Fig. 15); 4) tridentate (dorsal tooth divided in two) (Fig. 16).
6. Subocular sulcus: 0) absent to indistinct (Fig. 12); 1) present (Fig. 17).
7. Apical flagellomere of female: 0) simple; 1) with projections arising at outgrowth from surface (see Wahl and Gauld 1998: Fig. 2); 2) flattened apically and without setae (Fig. 18)
8. Antennal color of female: 0) more or less unicolorous; 1) with distinct light coloured median band.
9. Flagellum of male: 0) central flagellomeres lacking tyloids; 1) central flagellomeres with elliptical (Fig. 19) or raised, longitudinal ridge-like tyloids on ventral surface (Fig. 20).
10. Inner margin of eye: 0) not or only weakly emarginate (Figs 10, 12); 1) strongly emarginate near antennae.
11. Lateral ocellus: 0) small, separated from eye by 0.5× its diameter or greater; 1) enlarged, touching, or almost touching eye.

12. Gena: 0) simple; 1) denticulate (Fig. 21).
13. Occiput with medial notch near foramen magnum: 0) absent; 1) present (see Wahl and Gauld 1998: Figs 8–9).
14. Occipital carina: (0) joining hypostomal carina at a distance from mandible that is less than basal width of mandible (Fig. 1); 1) joins hypostomal carina at a distance from mandible greater than basal width of mandible; 2) runs directly to mandibular base.
15. Foramen magnum: 0) simple (Fig. 1); 1) laterally expanded (see Wahl and Gauld 1998: Fig. 11).
16. Maxillary palpus: 0) 5-segmented; 1) 4-segmented; 2) 3-segmented.
17. Maxillary palpus: 0) normal; 1) elongate, reaching to or beyond middle coxa.
18. Labial palpus: 0) 4-segmented; 1) 3-segmented.
19. Propleuron: 0) without lateroventral posteriorly-projecting lobe (Fig. 2); 1) with lateroventral posteriorly-projecting lobe (Fig. 22).
20. Epomia: 0) present as ridge ventro-anteriorly that crosses furrow dorsally (Fig. 2); 1) reduced to short central ridge across furrow (Fig. 23); 2) absent.
21. Mesoscutum: 0) smooth (Fig. 2); 1) with transverse rugae (Fig. 24).
22. Notaulus: 0) shallow or vestigial; 1) deeply impressed anteriorly (Fig. 2A); 2) absent.
23. Notaulus: 0) extending to 0.5× length of mesoscutum or less; 1) extending posteriorly past centre of mesoscutum but not joining other notaulus; 2) extending posteriorly past centre and joining either other notaulus or rugose medial area (Fig. 25); 3) absent.
24. Notaular crest or carina anterolateral to notaulus: 0) absent; 1) present (arrow in Fig. 26).
25. Epicnemial carina: 0) not curving anteriorly, vertical to around middle of pronotum; 1) curving to anterior of mesopleuron, around middle of pronotum (arrow in Fig. 27); 2) extending all the way to subtegular ridge (Fig. 2C); 3) present ventrally only (not extending dorsally to ventral edge of pronotum); 4) absent.
26. Sternaulus length: 0) present, less than 0.7× length of mesopleuron; 1) present, greater than or equal to 0.7× length of mesopleuron (Figs 2F, 28); 2) entirely absent.
27. Sternaulus curvature: 0) short, not reaching posterior end of mesopleuron (posterior curvature not scoreable); 1) posterior end ending dorsal to posterolateral corner of mesopleuron (Fig. 2F); 2) posterior end ending anterior to posterolateral corner of mesopleuron (arrow in Fig. 28).
28. Foveate groove of mesopleuron: 0) absent; 1) present (arrow in Fig. 29).
29. Mesopleural groove: 0) absent to incomplete; 1) complete to posterior margin of mesopleuron (“mg” in Fig. 30).
30. Posterior transverse carina of mesothoracic venter: 0) absent; 1) interrupted near anterior of middle coxa (gap indicated by arrow in Fig. 31); 2) complete (arrow in Fig. 32).
31. Metapostnotum: 0) posterolateral triangles present (Figs 3, 33); 1) posterolateral triangles absent.

32. Propodeum base: 0) without median tubercle; 1) with small, median tubercle (arrow in Fig. 34).
33. Propodeal spiracles: 0) separated from pleural carina by about minimum diameter of spiracle or more (Fig. 2); 1) separated from pleural carina by less than minimum diameter.
34. Propodeal spiracles: 0) round to sub-circular (less than 1.5× as long as high) (Figs 34, 35); 1) ovoid to elongate (1.5× as high as long or more) (Figs 2, 36).
35. Lateral profile of propodeum: 0) angulate with separate dorsal and posterior faces (Fig. 2); 1) rounded to flattened, without separate dorsal and posterior faces (Fig. 35).
36. Anterior transverse carina of propodeum: 0) complete (medially and sublaterally) (Fig. 3); 1) medial abscissa present, sublateral abscissae (= costulae) absent (Fig. 36); 2) median abscissa absent, sublateral abscissae present (Fig. 37); 3) completely absent (Fig. 40). Note: condition of the lateral abscissa was not coded because the presence of the spiracle makes scoring the condition in this region problematical.
37. Anterior transverse carina of propodeum: 0) medially angled (Fig. 3); 1) forming more or less smooth arc (Fig. 38). Note: if carina absent or incomplete so that angulation/curvature could not be scored, character is coded as “?”
38. Posterior transverse carina of propodeum: 0) complete (medially and sublaterally) (Figs 3, 36–38, 40); 1) medial abscissa present, sublateral abscissae absent; 2) median abscissa absent, sublateral abscissae present (areolar area confluent with petiolar area) (Fig. 39); 3) completely absent/ indistinguishable.
39. Posterior transverse carina of propodeum: 0) as strongly developed as other carinae; 1) conspicuously stronger than other carinae (Fig. 33). Note, if carina absent, coded as “?”
40. Posterior transverse carina: 0) angled (Fig. 3); 1) more or less continuous arc (Fig. 40). Note: if carina absent or angulation uncertain, coded as “?”
41. Anterior abscissa of medial longitudinal carina: 0) present, not fused (Fig. 3); 1) present, fused for entire length (arrow in Fig. 41); 2) absent (Fig. 40).
42. Median abscissa of medial longitudinal carina: 0) present, not fused (Fig. 3); 1) present, fused for entire length; 2) absent (Fig. 40).
43. Posterior abscissa of medial longitudinal carina: 0) present, not fused (Fig. 3); 1) present, fused for entire length; 2) absent (Fig. 40).
44. Anterior abscissa of lateral longitudinal carina: 0) present (Fig. 3); 1) absent (Fig. 38).
45. Median abscissa of lateral longitudinal carina: 0) present (Fig. 3); 1) absent (Fig. 40).
46. Posterior abscissa of lateral longitudinal carina: 0) present (Fig. 3); 1) absent (Fig. 37).
47. Propodeal surface reticulation: 0) smooth, without reticulation (Fig. 3); 1) mostly covered by reticulation that obscures carinae (Fig. 42).

48. Submetapleural carina: 0) complete, anterior section unmodified to slightly broadened (arrow in Fig. 43); 1) complete, anterior section abruptly broadened into a lobe (arrow in Fig. 44); 2) anteriorly present, not lobe-like (arrow in Fig. 45), posteriorly absent; 3) completely absent.
49. Height of ventral edge of metasomal foramen ("mf" in Figs 46, 47): 0) ventral in relation to dorsal edge of hind coxal foramen ("cf" in Fig. 46); 1) dorsal in relation to dorsal edge of hind coxal foramen ("cf" in Fig. 47).
50. Metacoxal cavity posteromedially: 0) separated from metasomal insertion by sclerotized bridge (Fig. 46); 1) confluent with metasomal insertion (arrow in Fig. 48 points to unsclerotized region joining metasomal and coxal foramina).
51. Fore wing vein *2m-cu*: 0) present (Fig. 4); 1) absent (Fig. 49).
52. Fore wing vein *2m-cu* posteriorly: 0) vertical (joining vein *Cu* at right angle) to slightly reclivous (Fig. 4); 1) inclivous (joining *Cu* at acute angle) (Fig. 50).
53. Fore wing vein *2m-cu*: 0) with two discrete bullae separated by small length of tubular vein (arrows in Fig. 50); 1) with single bulla (Figs 52–54).
54. Fore wing cell *I+2Rs* (areolet): 0) obliquely rhombic to subtriangular (Fig. 51); 1) rhombic to subrhombic (Fig. 52); 2) with vein *Rs* absent so only cross vein is distad *2m-cu* (Fig. 53); 3) with *3rs-m* absent so only cross vein is basad *2m-cu* (Fig. 50); 4) obliterated (vein *Rs* touching vein *M* so that veins *Rs* and *3rs-m* cannot be scored (Fig. 55); 5) symmetrically pentagonal (Fig. 4A) (vein *3rs-m* may be present or absent, but if absent, pentagonal nature of cell is evident) (e.g., Fig. 50); 6) large, roughly square, distal edge as high as proximal edge (Fig. 56); 7) irregularly pentagonal (Fig. 57).
55. Fore wing cell *I+2Rs* (areolet) veins: 0) similar thickness to other fore wing veins (Fig. 4); 1) abscissae of vein *Rs* and vein *M* that comprise areolet thickened relative to other fore wing veins (Fig. 58).
56. Fore wing cell *I+2Rs* (areolet): 0) sessile anteriorly (Figs 4A, 56–57); 1) petiolate anteriorly (Figs 51–52).
57. Antero-medial fore wing flexion line basally: 0) splitting anterior to *M* and anterior fold running anterior to *M* (forming bulla indicated by arrow) (Fig. 49); 1) anterior fold running posterior to *M* (creating bulla(e) in vein *2m-cu*) (Figs 50–57). Note: In ichneumonids (state 1), the flexion line never creates a bulla in the basal cross-vein of the areolet (whether open, closed or as in Ophioninae); whereas in braconids (state 0), this bulla is generally present (unlabelled arrow in Fig. 49).
58. Fore wing cell *2R1* (radial cell) posterior angle: 0) greater than 100 degrees (Fig. 4); 1) 90 degrees or less (Fig. 58).
59. Fore wing cell *1M+1R1*: 0) uniformly hirsute; 1) with small to large glabrous area that may have free sclerites (Fig. 59).
60. Fore wing vein *Rs+M* (ramellus): 0) complete (extending across all of cell *1M+1R1*) (Fig. 49); 1) incomplete (present only as short vein or stub) (Fig. 53); 2) completely absent (Fig. 4).

61. Fore wing vein *Icu-a*: 0) opposite, slightly proximal or slightly distad vein *M* (Fig. 4); 1) distad vein *M* by 0.5× length of *Icu-a* or greater (Fig. 58); 2) proximal to vein *M* by 0.3 length of *Icu-a* or greater (Fig. 60).
62. Hind wing vein *Irs-m*: 0) basal to separation of veins *R1* and *R_s* (Fig. 49); 1) opposite or apical to separation of veins *R1* and *R_s* (Fig. 4).
63. Hind wing vein *2/Cu*: 0) equidistant between *A* and *M*, closer to *A* or slightly closer to *M* (Fig. 4); 1) much closer to *M* than *A* (Fig. 61) or appearing to originate from *M*; 2) absent (Fig. 49).
64. Hind wing vein *M+Cu*: 0) complete (Fig. 62); 1) basal 0.6 spectral (Fig. 58).
65. Hind wing vein *M+Cu*: 0) straight to weakly arched (Fig. 61); 1) strongly arched (Fig. 62).
66. Hind wing basal hamuli: 0) distant from wing base on membrane or spectral vein; 1) close to wing base on spur of tubular vein; 2) absent.
67. Hind wing distal hamuli: 0) 1–3; 1) 4 or greater.
68. Apex of fore tibia: 0) without tooth; 1) with distinct tooth on dorsal margin (Fig. 63).
69. Fore tibia dorsal surface: 0) covered with uniform thickness of setae; 1) with uniform setae and sparse, much stouter spines (Fig. 64).
70. Middle tibial spurs: 0) two; 1) one.
71. Apex of middle and hind tibiae: 0) with common area of insertion for spurs and basitarsus; 1) with sclerotized bridge separating insertion areas (Fig. 65).
72. Female hind coxa: 0) simple, without furrow; 1) with inner surface near base with vertical basal furrow (Fig. 66).
73. Hind tibia: 0) covered with uniform thickness of setae; 1) with uniform setae and sparse, much stouter spines (Fig. 67).
74. Hind tibia: 0) with posterior face simple (not smooth and shining) and with moderately sparse fringe of setae (Fig. 68); 1) with posterior face smooth and shining and thick fringe of setae (Fig. 69).
75. Hind tibial spurs: 0) present; 1) absent.
76. T1 petiolar cross-section (measured at petiolar midpoint): 0) not petiolate or if petiolate not wider than high (height/ width = 1–1.2×); 1) wider than high (height/ width = 0.6–0.7×).
77. T1 spiracle location: 0) at or anterior to 0.6× length of segment; 1) posterior to 0.6× length of segment.
78. T1 glymma: 0) present and shallow (Fig. 70); 1) relatively deep, almost meeting at midline (Fig. 71); 2) absent.
79. First metasomal segment shape: 0) non-petiolate: more or less evenly broadened from near base to posterior end or, if more or less parallel-sided throughout, then clearly depressed and less than 2.0× as long as posteriorly wide (Fig. 72); 1) petiolate: anteriorly more or less parallel-sided and broadened posterior to spiracles or, if parallel-sided throughout, then more or less cylindrical and greater than 2.0× as posteriorly wide. (Fig. 73).
80. S1 length: 0) 0.6× length of T1 or less; 1) longer than 0.6× length of T1.

81. S1 fusion apically: 0) not fused to T1 (Fig. 74); 1) fused, but suture visible (Fig. 75); 2) fused, suture not visible.
82. Thyridium shape: 0) present, ovoid (Fig. 76); 1) present, linear (“th” in Fig. 77); 2) absent.
83. Thyridium location: 0) less than one length or diameter distant from anterior edge of T1 (Fig. 77); 1) greater than or equal to one length, width or diameter distant from anterior edge of T1 (Fig. 76).
84. Gastrocoelus: 0) absent; 1) present (“gs” in Fig. 77).
85. Pseudothyridium of T2: 0) present (“ps” in Fig. 78); 1) absent.
86. T2 sculpture: 0) smooth to granulate; 1) with clearly defined longitudinal rugulae.
87. T2 and T3 fusion: 0) separate, with flexion line allowing movement (Fig. 2); 1) fused, without a flexion line.
88. MS2 laterotergites: 0) creased and curved mesad under metasoma (“L2” in Fig. 79); 1) not separated by a crease (Fig. 80).
89. MS3 laterotergite: 0) separated by crease, often partially turned under (“L3” in Fig. 79, arrow points to crease); 1) not separated by crease (Fig. 80).
90. MS4 laterotergite: 0) separated by crease (at least basally), often turned under; 1) not separated by crease (Fig. 80).
91. T2–T4 sculpture: 0) each tergite uniformly sculptured; 1) posterior 0.2 of each tergite sculptured differently than anterior 0.8 (arrows in Fig. 81).
92. Apical segment of female metasoma: 0) short; 1) elongate with horn or boss (“h” in Fig. 82); 2) elongate without horn or boss (arrow in Fig. 83).
93. Posterior sternites of female: 0) without ovipositor guides; 1) with tuberculate ovipositor guides (arrows in Fig. 84).
94. Female hypopygium in lateral profile: 0) inconspicuous and uniformly sclerotized; 1) moderate length, regularly triangular in profile, uniformly sclerotized (Fig. 85); 2) moderate length, regularly triangular in profile, medially membranous (Fig. 86, arrow points to medial, membranous region); 3) extending far beyond apex of posterior tergites, strongly triangular in profile, uniformly sclerotized (Fig. 87).
95. Hind margin of female hypopygium: 0) simple; 1) with median apical notch (arrow in Fig. 88).
96. Ovipositor length: 0) longer than apical height of metasoma but shorter than metasoma; 1) shorter than or equal to apical height of metasoma; 2) longer than length of metasoma.
97. Ovipositor ventral valve: 0) with teeth apically (Fig. 89); 1) without teeth apically.
98. Ovipositor ventral valve: 0) not enclosing dorsal valve; 1) enclosing dorsal valve.
99. Ovipositor dorsal valve, apically: 0) simply tapered (Fig. 2); 1) with dorsal, sub-apical notch (arrow in Fig. 90); 2) slender and needle-like (Fig. 85); 3) simple with nodus (Fig. 91, arrow points to nodus); 4) weakly sclerotized.
100. T8 or T8+9 of male: 0) medially longitudinally divided (Fig. 92, arrow points to line of longitudinal division); 1) not medially, longitudinally divided.

101. Hypopygium of male: 0) short and apically truncate; 1) elongate and scoop-like (Fig. 93).
102. Gonoforceps: 0) simple (“gon” in Fig. 92; 1) apically long and rod-like (Fig. 94).
103. Apical 0.5 of aedeagus: 0) subcylindrical and slightly to strongly clubbed (Fig. 95); 1) strongly flattened (Fig. 96).
104. Ovaries: 0) bohrertypus of Pampel (1913) (i.e., relatively low number of ovarioles and short lateral oviducts); 1) Ophion-typus of Pampel (large number of ovarioles and lateral oviducts 1–2 times as long as ovaries) (see Wahl 1991: Fig. 2).
105. Larval epistomal suture: 0) unsclerotized (Fig. 97); 1) partially sclerotized, medially incomplete (Fig. 6r); 2) completely sclerotized forming epistomal band (Figs 99, 101).
106. Larval hypostoma and pleurostoma: 0) not laterally expanded (Fig. 6a, b); 1) laterally expanded (Fig. 99).
107. Larval pleurostoma location: 0) inferior mandibular process dorsad or opposite to dorsal margin of labial sclerite (Fig. 6a, b); 1) shifted ventrally inferior to mandibular process opposite labial palpus (Fig. 100).
108. Larval labral sclerite: 0) present (Figs 6f, 7f); 1) absent (Fig. 97).
109. Larval mandible shape: 0) triangular, auxiliary tooth present or absent (Figs 6m, 7m); 1) cone shaped and with small apical tooth (Fig. 111, mandible in upper left); 2) bidentate, teeth subequal (Fig. 101); 3) reduced so that only apex of blade is present (Fig. 100); 4) absent.
110. Larval mandible with accessory teeth: 0) absent (Fig. 97); 1) present (Fig. 6m).
111. Larval mandible sclerotization: 0) uniformly sclerotized (Fig. 6m); 1) blade weakly sclerotized (base only or all except apex) (“m” in Fig. 100).
112. Larval mandibular blade denticles: 0) present on entire dorsal and ventral margins (Fig. 102); 1) present only on entire dorsal margin (Fig. 98); 2) absent on both dorsal and ventral margins (Fig. 97); 3) restricted to apex of dorsal and ventral margins; 4) mandible completely absent (Fig. 106).
113. Larval mandible, spines at base of blades: 0) juncture of base and blade without long, horizontal spines (Figs 97, 98); 1) juncture of base and blade with long (> 2× blade length) horizontal spines (Fig. 6m).
114. Larval posterior struts of inferior mandibular processes: 0) short (as long as dorsal struts) and not connected by band (Fig. 6k); 1) long (> 2× length of anterior struts) and connected by band (the latter indicated by an arrow in Fig. 103).
115. Larval hypostoma length: 0) long (>2 × as long as hypostomal spur) (Fig. 6b relative to 6c); 1) reduced (1–1.5 × as long as hypostomal spur); 2) absent or present only as a rudimentary stub (Fig. 103).
116. Larval hypostoma, lateral end: 0) simple/ undivided (Fig. 6b) divided as two bands, or with one upcurved extension; 1) divided into two bands, ventral band long, robust, downcurved (arrow in Fig. 104).
117. Larval hypostomal spur: 0) normal, about 2× as long as basal width or longer (Fig. 6c); 1) reduced, about as long as basal width (Fig. 97); 2) absent or only a rudimentary stub (Figs 99, 100).

118. Larval hypostomal spur meeting stipital sclerite: 0) near middle to lateral end of stipital sclerite (Fig. 6c, 6d); 1) near median end of stipital sclerite (Fig. 102); 2) fused and forming hypostomal-stipital plate (Fig. 105); 3) hypostomal-stipital plate reduced to narrow strip (Fig. 106); 4) fused in L-shaped structure (Fig. 107); 5) absent (Fig. 112).
119. Larval stipital sclerite orientation: 0) oriented so that lateral end at about right angle to labial sclerite (Figs 97, 98); 1) dorso-ventrally angled, lateral end near or on hypostoma (Fig. 99); 2) absent.
120. Larval stipital sclerite lateral end: 0) unmodified (Fig. 6d); 1) with plate-like expansion (Fig. 108).
121. Larval cardo: 0) unsclerotized (Fig. 6j); 1) present as lightly sclerotized oval (Fig. 104).
122. Larval maxillary apex: 0) unsclerotized (Fig. 6p); 1) sclerotized.
123. Larval maxillary and labial palpi sensilla: 0) maxillary bearing one to two, labial bearing one to three (Fig. 6i, 6h); 1) each bearing three (Fig. 103); 2) each bearing four to five (Fig. 109).
124. Larval labial sclerite shape: 0) quadrate (Fig. 6e); 1) circular (Fig. 104) to elongate-ovoid (Fig. 97); 2) absent (Fig. 109).
125. Larval labial sclerite dimensions: 0) about as long as wide, length of ventral portion/ total length = 0.2–0.3 (Fig. 98); 1) 1.4–1.7× as long as wide, length of ventral portion/ total length = 0.4–0.7× (Fig. 97).
126. Larval labial sclerite ventral margin: 0) relatively unmodified (may be lobes, minor scalloping, etc.) (Fig. 6e); 1) produced as spine (Fig. 100).
127. Larval prelabial sclerite: 0) absent (Fig. 6); 1) present as transverse band (arrow in Fig. 110); 2) present as triangular to Y-shaped structure (“ps” in Fig. 97).
128. Larval prelabium, number of sensilla: 0) 6 (Fig. 108); 1) 8 or more (Fig. 104).
129. Larval sclerotized plate ventral to labial sclerite: 0) absent (Fig. 6); 1) present (“sp” in Fig. 98).
130. Larval clypeolabral plate location: 0) absent (Fig. 6); 1) present, not contacting pleurostoma (“cl” in Fig. 100); 2) touching pleurostoma (Fig. 109).
131. Larval antenna: 0) present and with central papillus present (Figs 6n, 102); 1) present and lacking central papillus (Figs 104, 108); 2) absent.
132. Larval spiracles: 0) present, closing apparatus separated from atrium by section of trachea (Fig. 103b); 1) present, closing apparatus adjacent to atrium (Fig. 109); 2) present, closing apparatus absent; 3) completely absent.
133. Larval salivary orifice: 0) transverse or ovoid (Figs 105, 107); 1) u-shaped (Figs 6g, 97).
134. Egg: 0) without stalk; 1) with chorionic stalk (Fig. 113); 2) egg with a wide, pedunculate, ventral protrusion and an apical, sinuous stalk (Fig. 114); 3) stalk formed from hardened secretion from female (Figs 115, 116).
135. Egg stalk anchor: 0) anchor absent or entire stalk absent; 1) with tryphonine-like anchor (Fig. 113); 2) with eucerotine disk-like anchor (Fig. 116).
136. Exit of egg from body: 0) egg travels down lumen of ovipositor; 1) egg exits from hole ventral to ovipositor, stalk goes down ovipositor; 2) entire egg exits from hole ventral to ovipositor.

137. Biological mode (timing of larval maturation): 0) idiobiont; 1) koinobiont.
138. Biological mode (location of development): 0) ectoparasitoid; 1) endoparasitoid; 2) inside hind gut with final ectoparasitoid phase AND pupate inside host cocoon.
139. Host/ source of larval nutrition: 0) phytophagous (at least facultatively after consuming insect host); 1) Hymenoptera; 2) Lepidoptera; 3) Coleoptera; 4) Diptera; 5) Araeneae; 6) Trichoptera; 7) Neuroptera; 8) egg predators.
140. Oviposition location: 0) through lignified plant tissue; 1) through non-lignified plant or gall tissue; 2) in leaf rolls, cases and other plant tissues held by silk; 3) in silken bags or sacs; 4) into or onto exposed larval/ pupal hosts; 5) into ground nests; 6) into trichopteran tubes; 7) into exposed eggs; 8) on to leaf; 9) into host in host.
141. Oviposition/emergence stages: 0) eggs (predators); 1) larval-larval (not last instar); 2) pupa-pupa; 3) egg-larval; 4) immature spider - adult spider; 5) larval-larval (last instar); 6) larval-pupal; 7) egg-pupal; 8) leaf-pupa.

Phylogenetics

Parsimony analysis

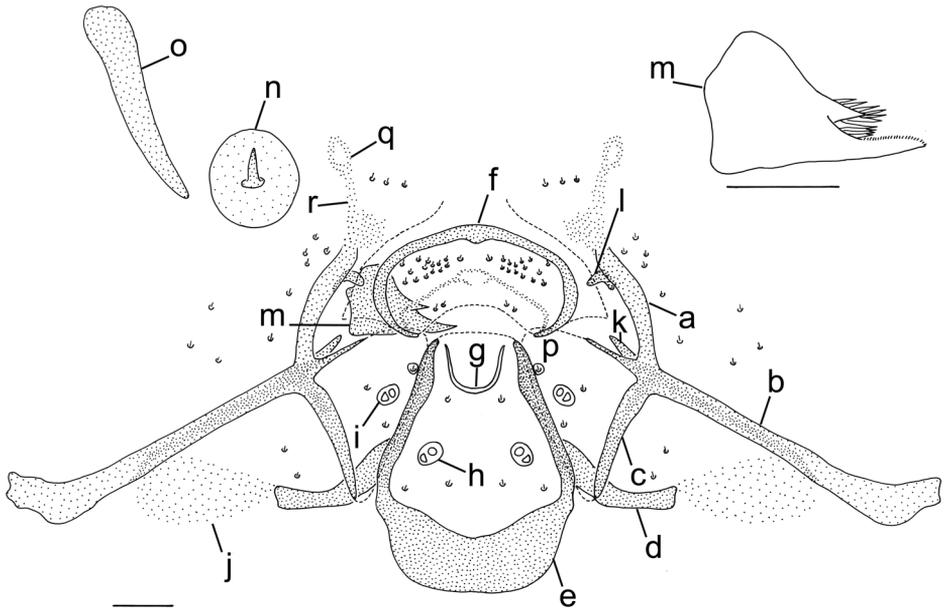
Total-evidence

The total-evidence parsimony analysis found 1728 equally parsimonious trees of length 9917 (C.I. = 0.15, R.I. = 0.44). In the strict consensus tree (Fig. 117), 14 nodes collapsed. Table 3 (column “Pars. (all)”) provides a summary of the taxa that were recovered as unequivocally monophyletic. In summary, of the 29 groupings included in Table 3, 15 were monophyletic and a further 8 groupings would be monophyletic with inclusion or exclusion of one or more problematical/ equivocally classified taxa as described in footnotes. *Aplomerus* (Xoridinae) was sister group to all other Ichneumonidae, (*Odontocolon* + *Xorides*) was sister group to all except for *Aplomerus*, and Orthopelmatinae (*Orthopelma mediator* Thunberg) was sister group to all taxa except the three Xoridinae. The remainder of the subfamilies were arranged in three groupings. The sister group to the other two was the Ophioniformes of Quicke et al. (2009) comprised of 17 subfamilies. The second group was equivalent to the Pimpliformes of Quicke et al. (2009). The third group was the Ichneumoniformes s.l., which was comprised of Ichneumoniformes s.s. of Wahl (1993a) i.e., Brachycyrtinae + Cryptinae (including Ateleutinae and Phygadeuontinae) + Ichneumoninae (including *Alomya*), as well as Adelognathinae, Agriotypinae, Claseinae, Eucerotinae, Labeninae, Microleptinae and Pedunculinae. Placement and relationships of subfamilies within these three groupings will be discussed in the section Support/relationships of taxa (below). The average consistency indices for the different character types were as follows: adult (0.24), larval (0.41), egg (0.80), biological (0.22) and molecular (0.04).

Table 2. Data matrix for morphological character states of Ichneumonidae and outgroup taxa. Key to the letters in matrix below: a=0/1; b=0/2; c=0/3; d=1/2; e=1/3; f=1/4; g=1/5; h=2/3; k=2/4; m=2/6; n=3/4; p=3/7; q=5/6; r=6/7; s=0/1/3; t=1/5/6; u=2/6/7; v=5/6/7; w=2/5/6/7; x=3/5/6/7.

Taxon	1	2	3	4	5	6	7
<i>Doryctes erythronelidus</i>	1	2	3	4	5	6	7
<i>Rhyssalus</i> sp.	0	0	0	0	0	0	0
<i>Aleodes terminalis</i>	0	0	0	0	0	0	0
<i>Spilopteron occupatale</i>	0	0	0	0	0	0	0
<i>Colocentrus rufus</i>	0	0	0	0	0	0	0
<i>Adelognathus</i> sp.	0	0	0	0	0	0	0
<i>Agriotypus armatus</i>	0	0	0	0	0	0	0
<i>Anomalus pisticome</i>	0	0	0	0	0	0	0
<i>Therion texanum</i>	0	0	0	0	0	0	0
<i>Lissonota scutellaris</i>	0	0	0	0	0	0	0
<i>Exeastes bioculatus</i>	0	0	0	0	0	0	0
<i>Apophua simplicipes</i>	0	0	0	0	0	0	0
<i>Spheladon phoxopteridis</i>	0	0	0	0	0	0	0
<i>Brachytritus wardae</i>	0	1	0	0	0	0	0
<i>Bathyplectes infernalis</i>	0	1	0	0	0	0	0
<i>Campoplex sonorensis</i>	0	1	0	0	0	0	0
<i>Campoplex</i> sp.	0	1	0	0	0	0	0
<i>Casiniaria grandis</i>	0	1	0	0	0	0	0
<i>Dusona egregia</i>	0	1	0	0	0	0	0
<i>Hypooster</i> sp.	0	1	0	0	0	0	0
<i>Oleiscampe</i> sp.	0	1	0	0	0	0	0
<i>Rhinophactona macrocephala</i>	0	0	0	0	0	0	0
<i>Clasis</i> sp. nov.	0	0	0	0	0	0	0
<i>Collyria catoptron</i>	0	0	0	0	0	0	0
<i>Epilhosoma pyralidis</i>	0	0	0	0	0	0	0
<i>Xiphosomella setoni</i>	0	0	0	0	0	0	0
<i>Agnocryptus chichimecus</i>	0	0	0	0	0	0	0
<i>Ateleute</i> sp. nov.	0	0	0	0	0	0	0
<i>Barycyrtus texanus</i>	0	0	0	0	0	0	0
<i>Diapetimorpha brunnea</i>	0	0	0	0	0	0	0
<i>Echihrus reluctator</i>	0	0	0	0	0	0	0
<i>Lymexum orbis</i>	0	0	0	0	0	0	0

Taxon	1	2	3	4	5	6	7
<i>Plegiortyx concinnus</i>	1	2	3	4	5	6	7
<i>Dilopharius atomitus</i>	0	1	0	0	0	1	0
<i>Cyclolabus impressus</i>	0	1	0	0	0	1	0
<i>Linyx eshortator</i>	0	1	0	0	0	1	0
<i>Groeta anguina</i>	0	0	0	0	0	0	0
<i>Labium</i> sp.	0	1	0	0	0	0	0
<i>Apachoneura</i> sp.	1	0	0	0	0	0	0
<i>Labena gullator</i>	1	0	0	0	0	0	0
<i>Praeciloryptus nigromaculatus</i>	0	0	0	0	0	0	0
<i>Lycorina glaucumata</i>	0	0	0	0	0	0	0
<i>Asiophrona</i> sp. nov.	0	1	0	0	0	0	0
<i>Chineater mansueti</i>	0	1	0	0	0	0	0
<i>Cidaphna pansicoidea</i>	0	1	0	0	0	0	0
<i>Lepidiana collaris</i>	0	1	0	0	0	0	0
<i>Mesochorus</i> sp.	0	1	0	0	0	0	0
<i>Exochus seminifis</i>	0	1	0	0	0	0	0
<i>Metopijs pollinctorius</i>	0	1	0	0	0	0	0
<i>Scolomus</i> sp.	0	1	0	0	0	0	0
<i>Seticomata terminalis</i>	0	1	0	0	0	0	0
<i>Microleptes</i> sp.	0	0	0	0	0	0	0
<i>Neorhacodes ensitini</i>	0	0	0	0	0	0	0
<i>Chriades</i> sp.	0	0	0	0	0	0	0
<i>Nonnus</i> sp.	0	0	0	0	0	0	0
<i>Enicospilus flavostigma</i>	0	0	0	0	0	0	0
<i>Hellwigia obscura</i>	1	0	0	0	0	0	0
<i>Ophiom</i> sp.	0	0	0	0	0	0	0
<i>Skiaxys</i> sp.	0	0	0	0	0	0	0
<i>Thyreodon</i> sp.	0	0	0	0	0	0	0
<i>Megastylus</i> sp. nov.	0	0	0	0	0	0	0
<i>Orthocentrus</i> sp.	0	0	0	0	0	0	0
<i>Proctius speciosus</i>	0	0	0	0	0	0	0
<i>Orthopelma mediator</i>	0	0	0	0	0	0	0
<i>Oxytorus albopluralis</i>	0	0	0	0	0	0	0
<i>Pedunculatus</i> sp. nov.	0	0	0	0	0	0	0
<i>Perithous divinator</i>	0	0	0	0	0	0	0



- | | |
|----------------------|--|
| a. pleurostoma | j. cardo |
| b. hypostoma | k. inferior mandibular processes |
| c. hypostomal spur | l. superior mandibular process |
| d. stipital sclerite | m. mandible |
| e. labial sclerite | n. antenna (with central papillus present) |
| f. labral sclerite | o. parietal band (= ocular line) |
| g. salivary orifice | p. maxillary apex |
| h. labial palpus | q. anterior tentorial pit |
| i. maxillary palpus | r. epistoma |

Figure 6. Cephalic sclerites of final larval instar, *Xorides* sp. Scale bars: 1mm.

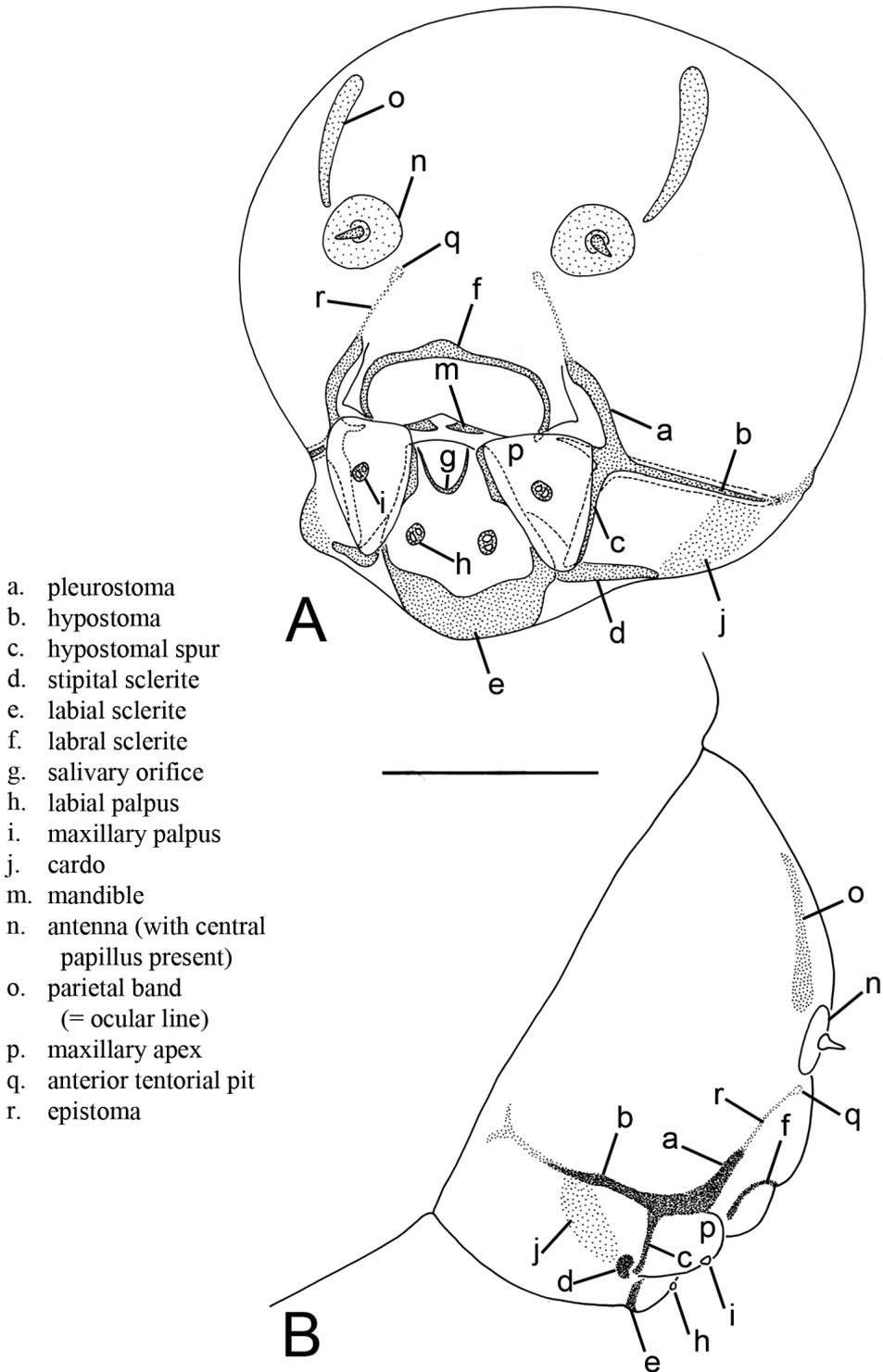
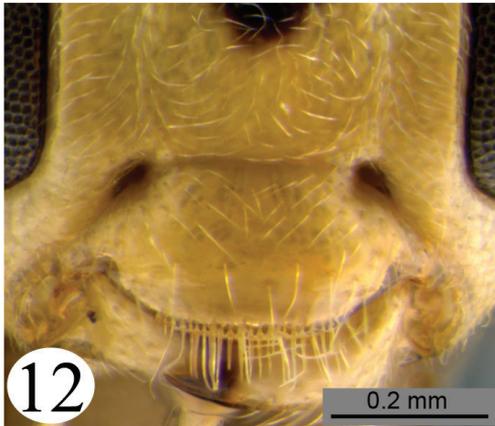
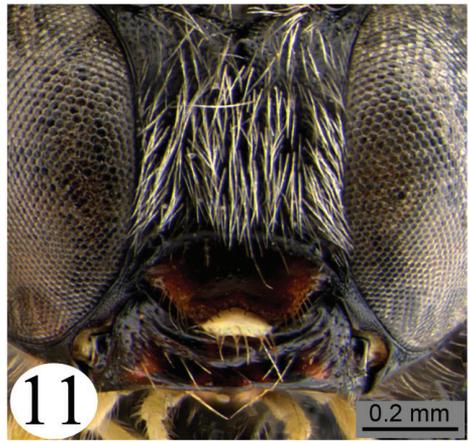
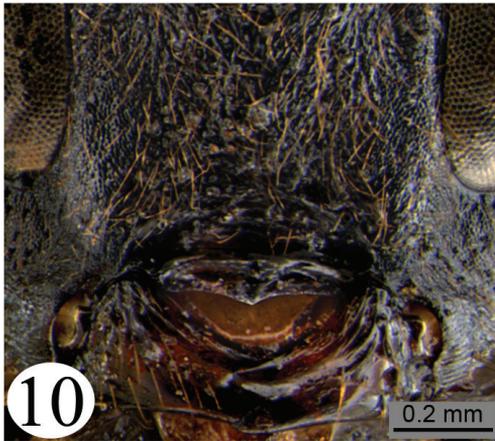
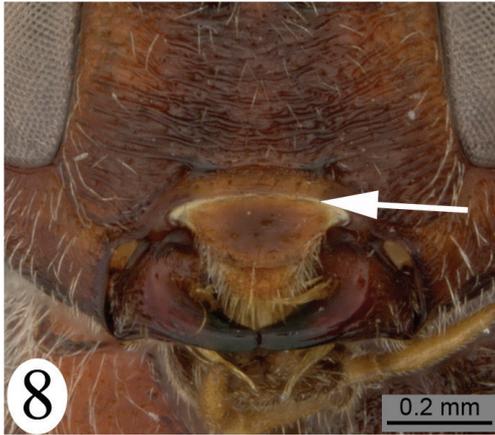
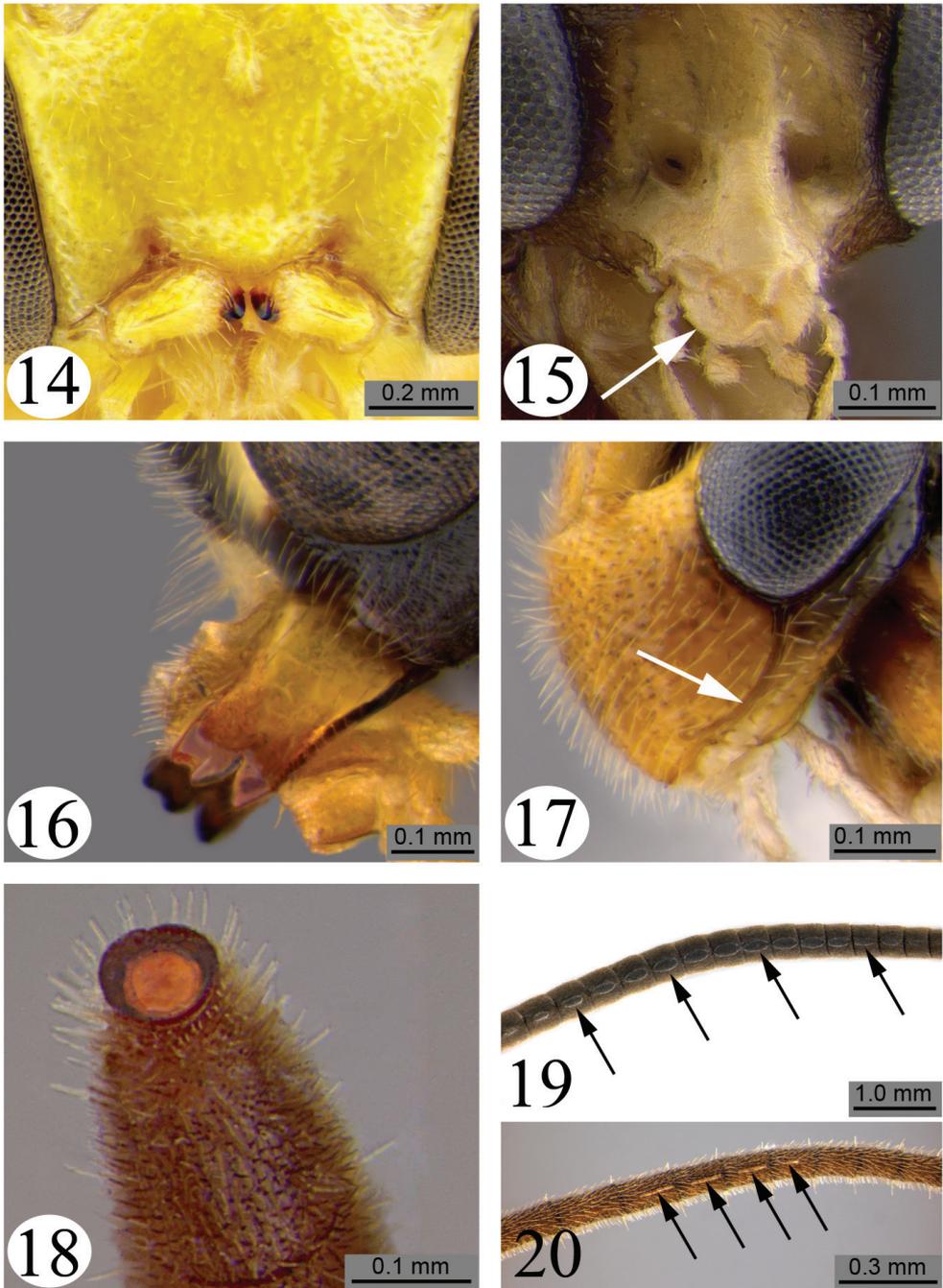


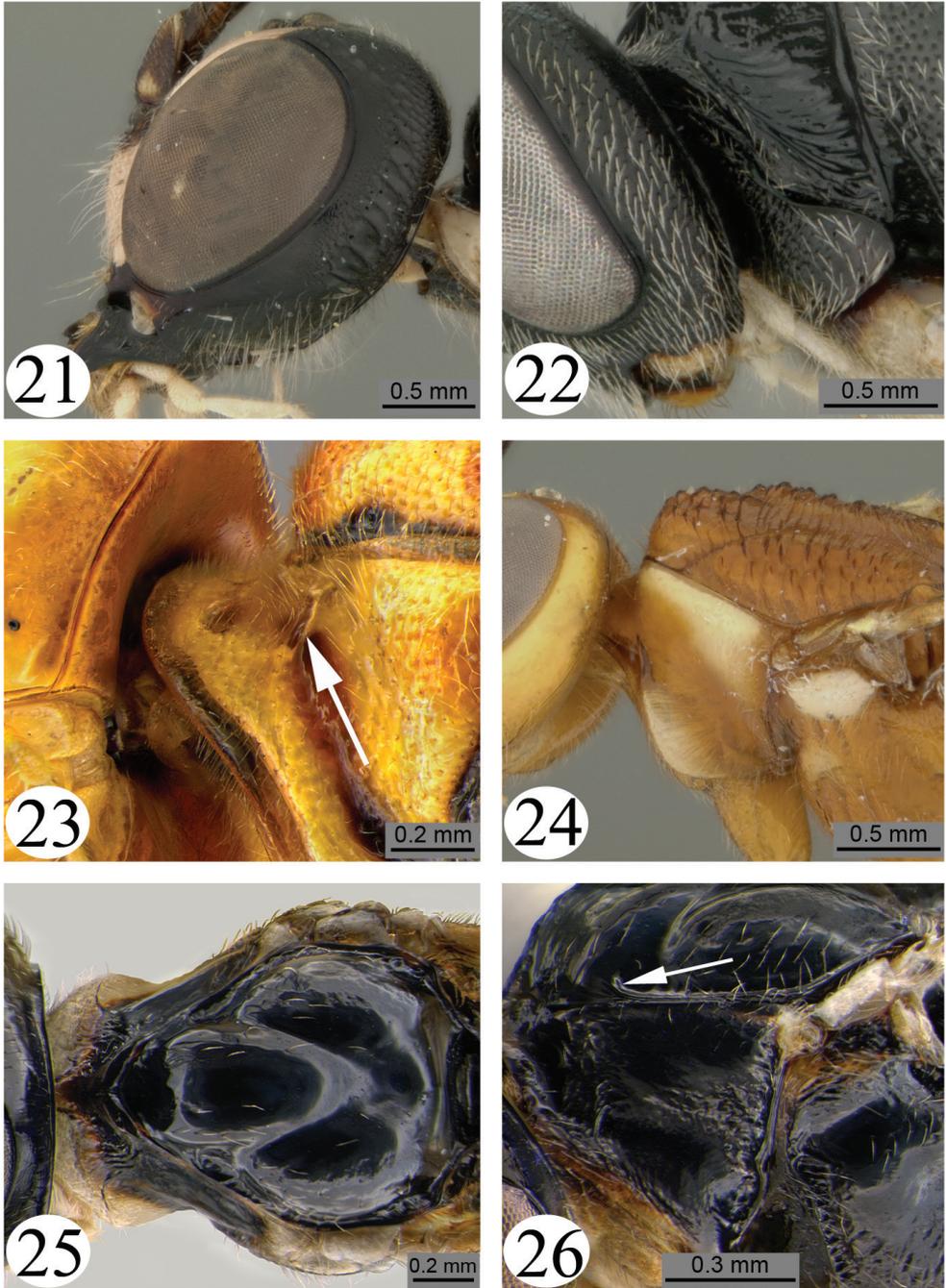
Figure 7. Final larval instar, anterior of whole larva, *Xorides* sp. **A** antero-lateral view **B** lateral view.



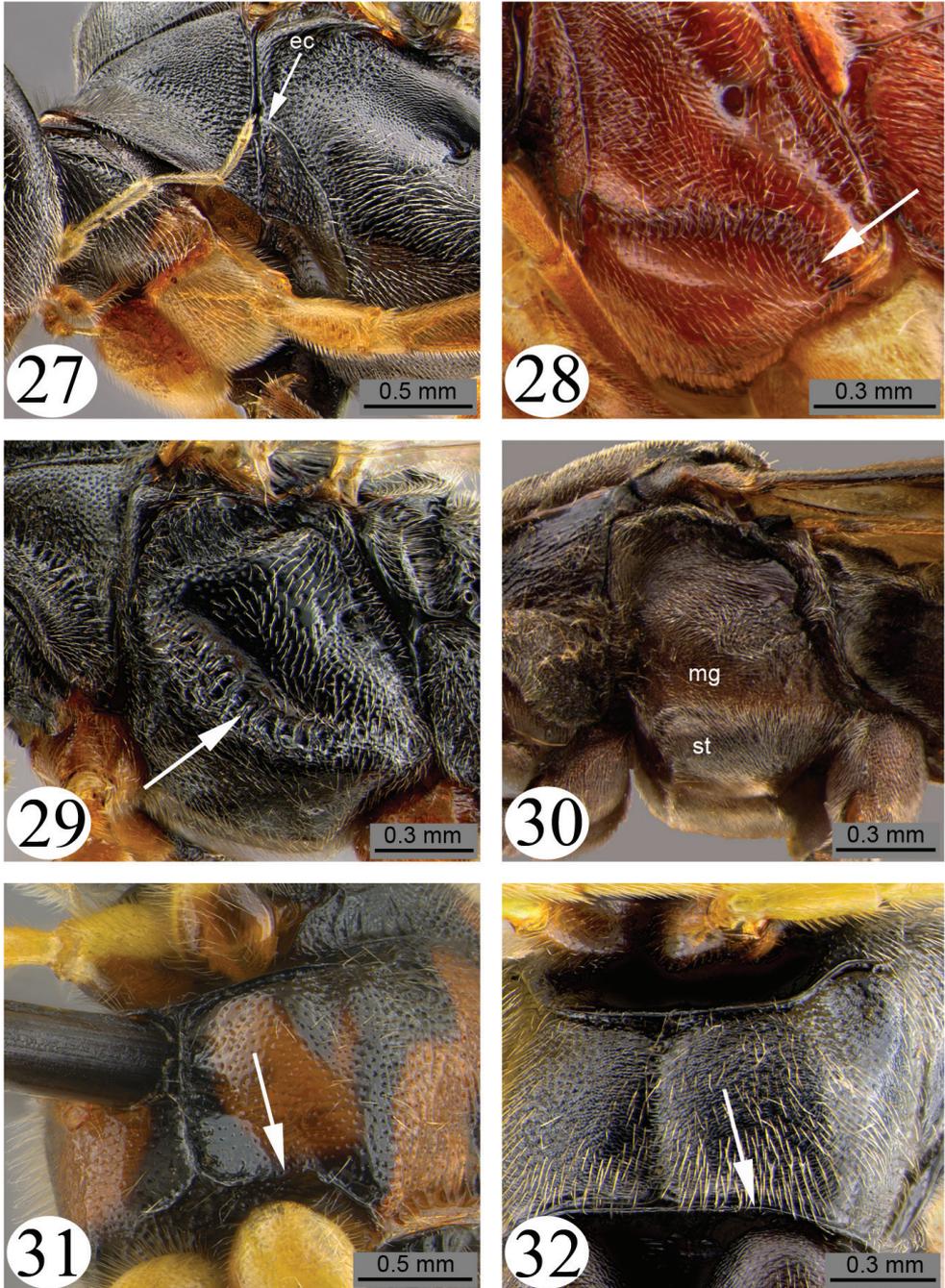
Figures 8–13. Head. **8** *Xorides stigmapterus*, anterior view. Arrow indicates division of clypeus into basal and apical parts **9** *Hyposoter* sp., anterolateral view **10–13** Anterior view **10** *Echthrus reluctator* **11** *Doliichomitus irritator* **12** *Hercus fontinalis* **13** *Neoxorides caryae*.



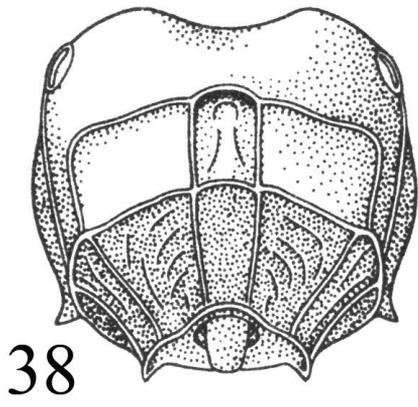
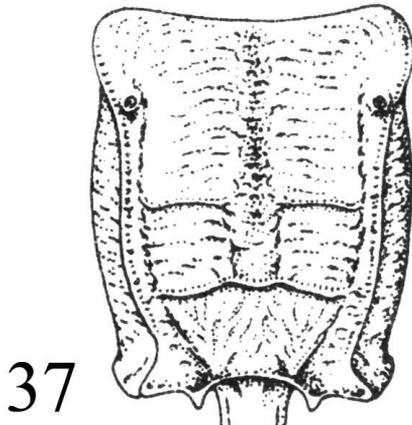
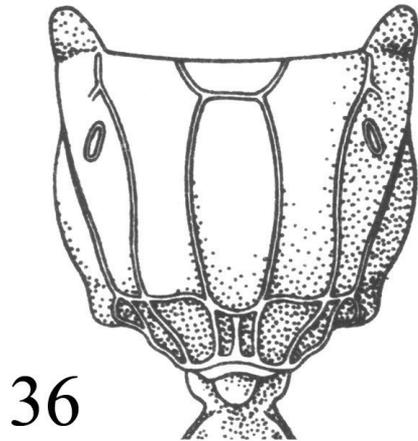
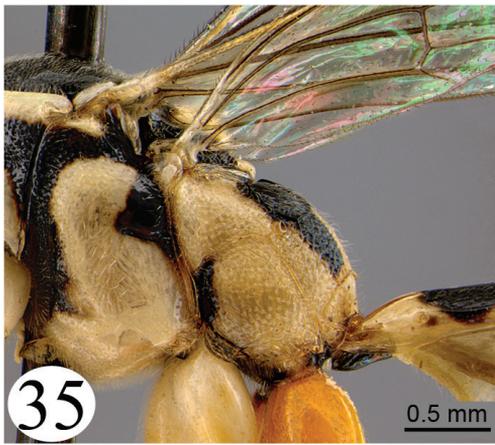
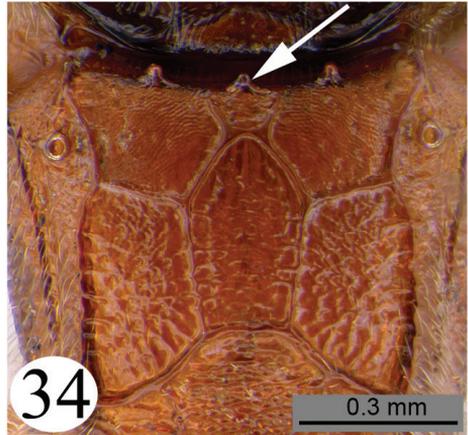
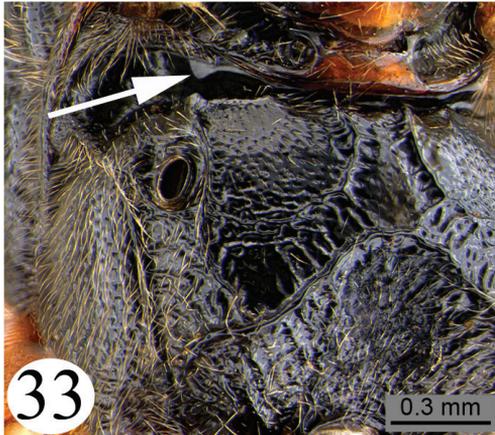
Figures 14–20. 14–15 Head, anterior view 14 *Skiapus* sp 15 *Hybrizon rileyi* Arrow indicates reduced mandible 16–17 Head, lateral view 16 *Diplazon lactatorius* 17 *Orthocentrus* sp. Arrow indicates subocular groove 18–20 Antennae 18 *Labena grillator*, apical flagellomere 19–20 Flagellum, lateral view, arrows indicate longitudinal tyloids 19 *Protichneumon grandis* 20 *Lymeon orbis* (Say).



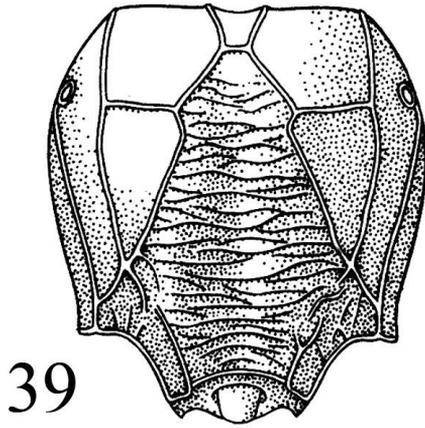
Figures 21–26. **21** *Podoschistus vittifrons* (Cresson), head, lateral view **22** *Venturia sokanakiakorum* (Viereck), head and mesosoma, lateral view, showing ventral lobe of propleuron **23** *Labena grillator*, pronotum, lateral view. Arrow indicates epomia **24** *Rhysella perfulva* Porter, head and mesosoma, lateral view **25–26** *Diacritus incompletus* **25** Mesosoma, dorsal view **26** Mesosoma, lateral view. Arrow indicates notaular crest.



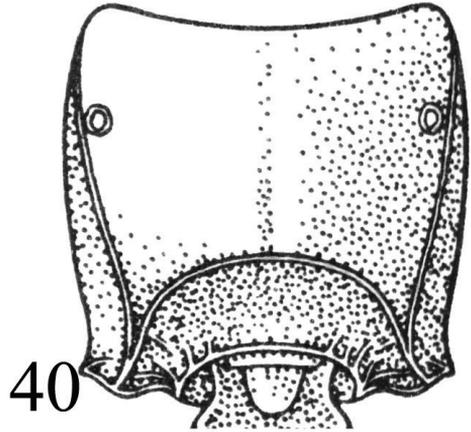
Figures 27–32. 27–30 Mesosoma, lateral view **27** *Rhimphoctona macrocephala*. *ec* = epicnemial carina **28** *Diapetimorpha brunnea* Townes. Arrow indicates sternaulus curving ventrally anterior to posterolateral corner **29** *Stethantyx nearctica*. Arrow indicates foveate groove **30** *Agriotypus armatus*. *mg* = mesopleural groove, *st* = sternaulus **31–32** Mesosternum, ventral view **31** *Therion longipes* (Provancher). Arrow indicates incomplete posterior transverse carina **32** *Dusona egregia*. Arrow indicates complete posterior transverse carina.



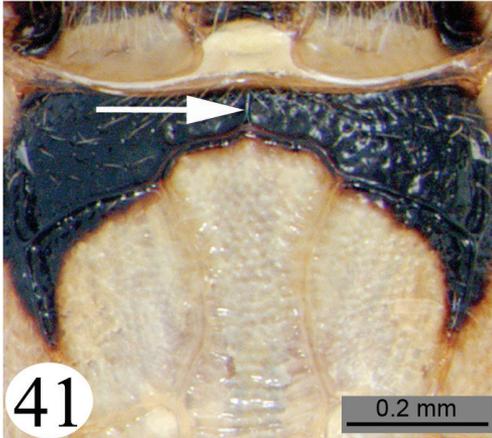
Figures 33–38. Propodeum. **33** *Polytribax contiguus* (Cresson), dorsolateral view. Arrow indicates posterolateral triangle of metanotum **34** *Centeterus euryptychiae*, dorsal view. Arrow indicates median tubercle at base of propodeum **35** *Sphelodon phoxopteridis*, lateral view **36–38** Dorsal view (re-drawn after Townes 1969, 1970a, 1971) **36** *Aplomerus tibialis* (Provancher) **37** *Atelete tsiriria* (Seyrig) **38** *Ophion flavidus* Brullé.



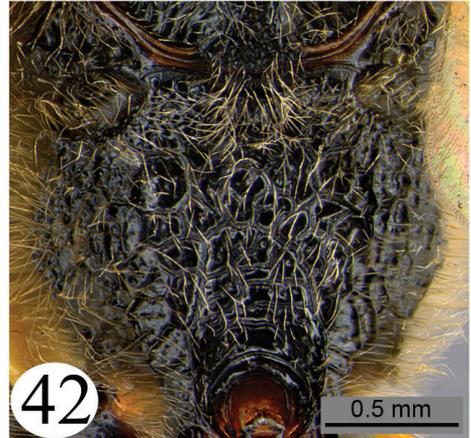
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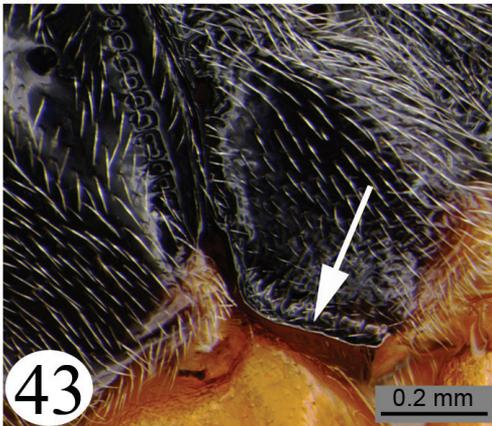
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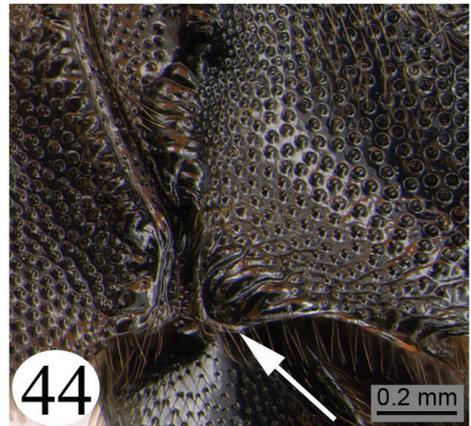
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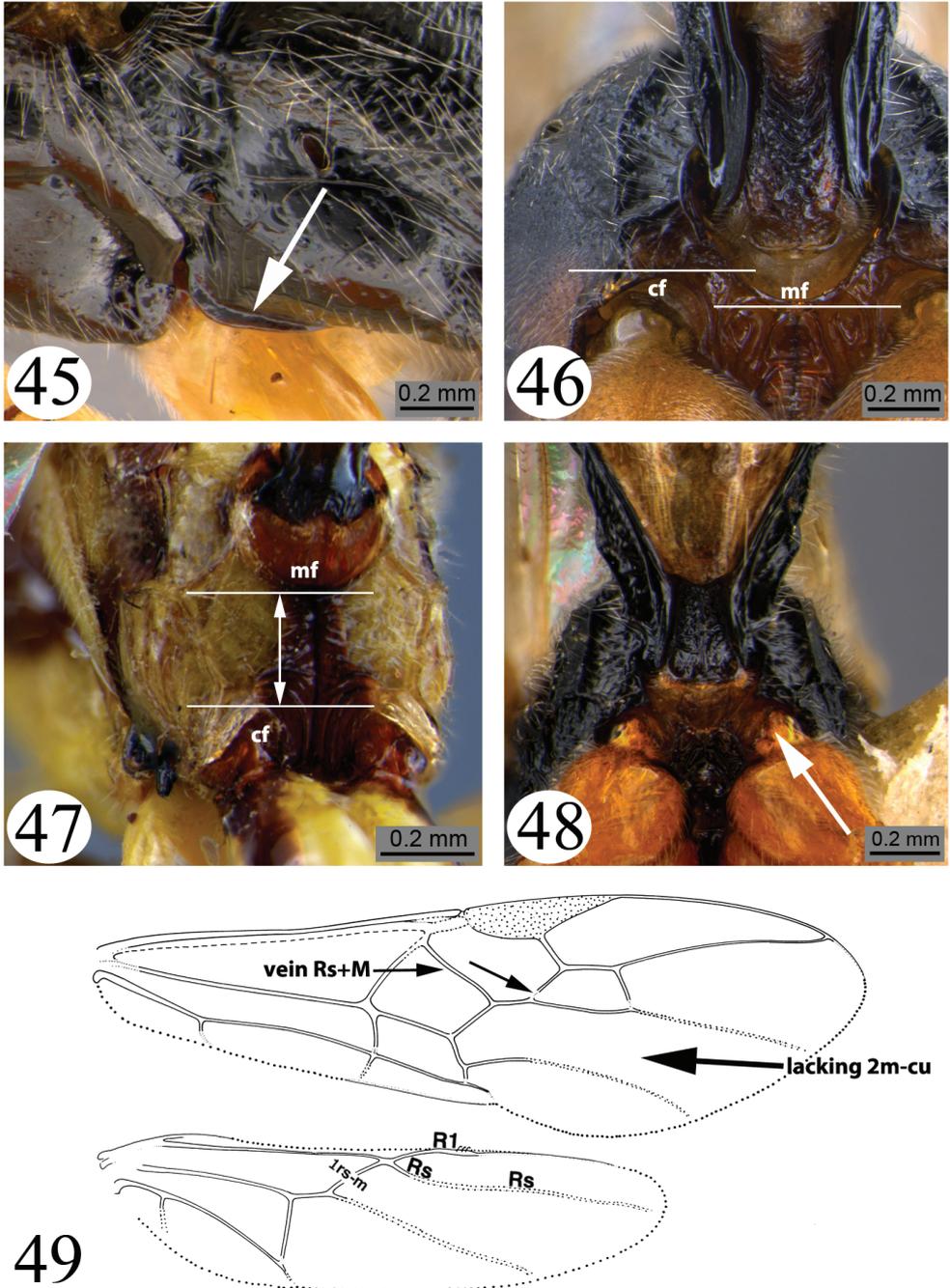


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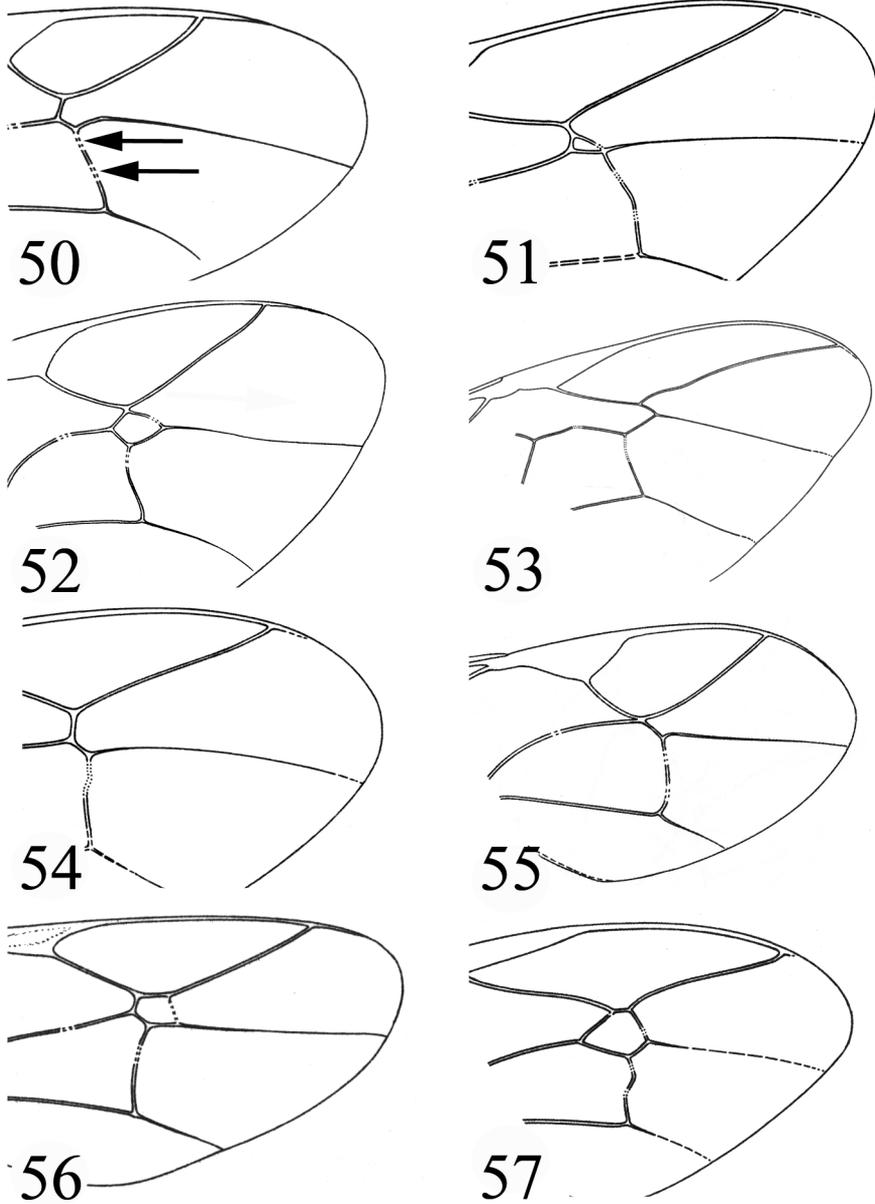


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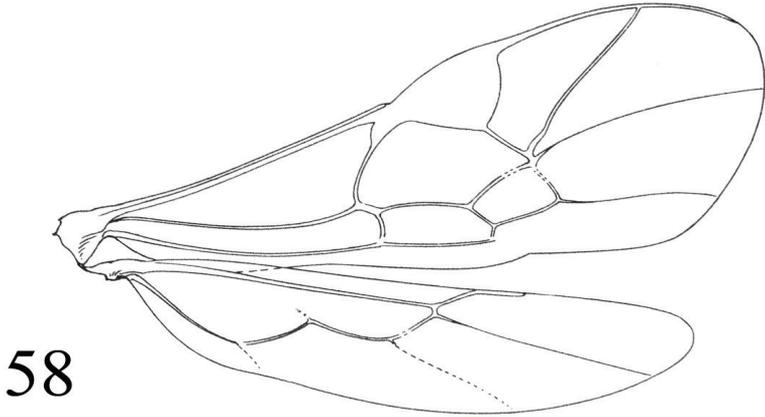
Figures 39–44. 39–42 Propodeum, dorsal view 39 *Pyracmon hyalinus* (re-drawn after Townes 1970b) 40 *Lissonota lineolaris* (Gmelin) (re-drawn after Townes 1970b) 41 *Brachycyrtus wardae*. Arrow indicates fused anterior abscissa of medial longitudinal carina 42 *Therion longipes* (Provancher) 43–44 Metapleuron, lateral view 43 *Pimpla aequalis* Provancher. Arrow indicates submetapleural carina 44 *Exetastes fornicator* (Fabricius). Arrow indicates anterior lobe of submetapleural carina.



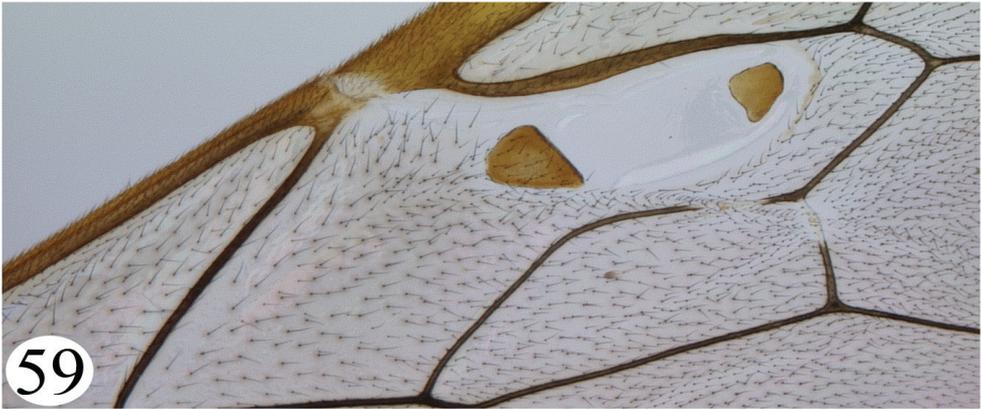
Figures 45–49. **45** *Dolichomitus irritator*, mesopleuron and metapleuron, lateral view. Arrow indicates submetapleural carina **46–48** Mesosoma and metasoma, ventroposterior view. Line above *cf*= dorsal edge of coxal foramen, line below *mf*= ventral edge of metasomal foramen **46** *Lissonota scutellaris* **47** *Apecho-neura* sp. **48** *Polyblastus pedalis* (Cresson). Arrow in 48 indicates unsclerotized region joining metasomal and coxal foramina **49** Wings, *Helcon* sp. (Braconidae) (modified from Goulet and Huber 1993). Unlabeled arrow indicates antero-medial flexion line.



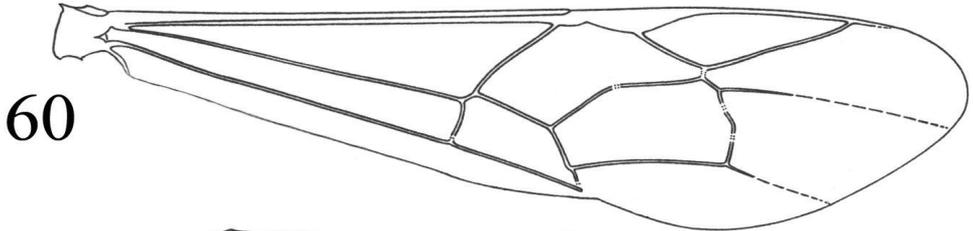
Figures 50–57. Fore wing (modified from Townes 1969, 1970a, 1970b, 1971) **50** *Mastrus acitulatus*. Arrows indicate bullae in vein *2m-cu* **51** *Phytodietus gelitorius* (Thunberg) **52** *Mesochorus* sp. **53** *Ophion flavidus* **54** *Glypta erratica* Cresson **55** *Proclitus* sp. **56** *Ateleute tsiriria* **57** *Labena grallator*.



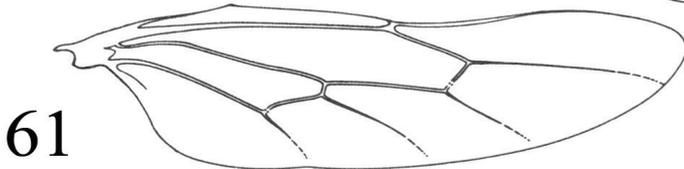
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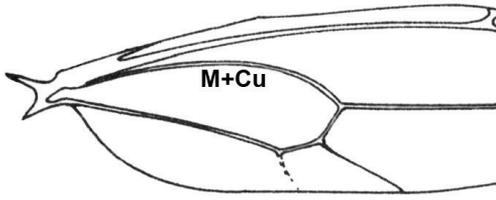


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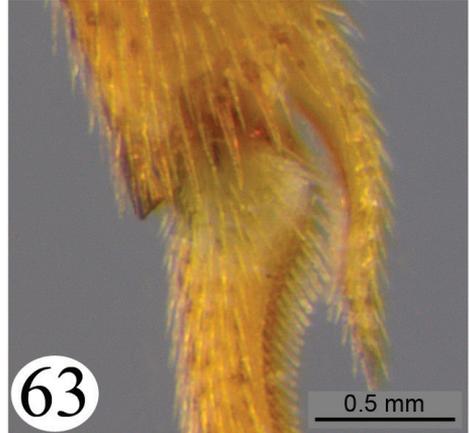


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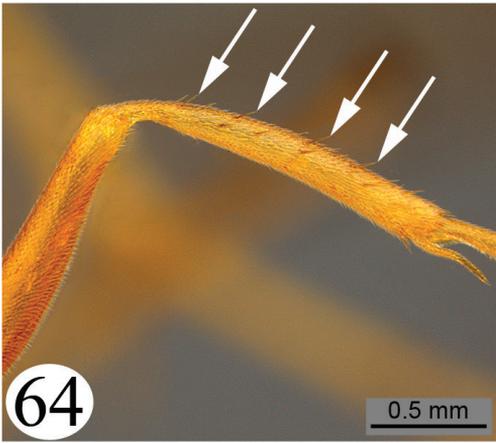
Figures 58–61. Wings. **58** *Allophrys oculata* (Ashmead), fore and hind wings **59** *Enicospilus purgatus* (Say), fore wing showing sclerites in cell 1M + 1R1 **60** *Aplomerus tibialis*, fore wing **61** *Exetastes fornicator*, hind wing.



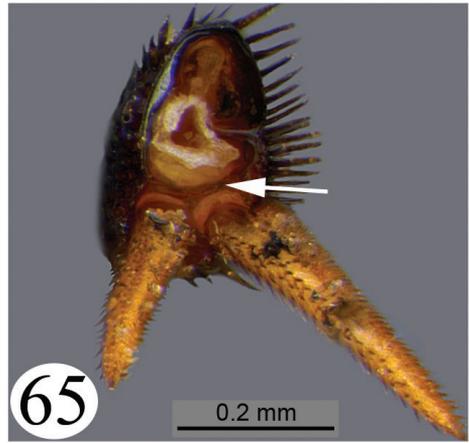
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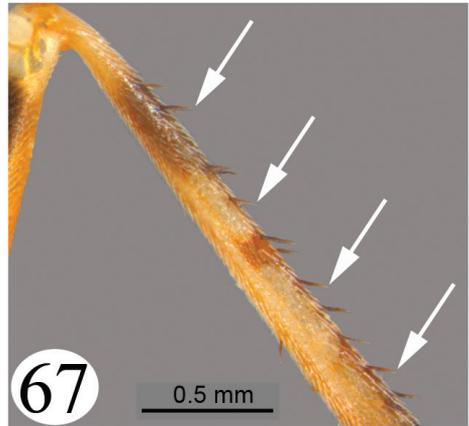
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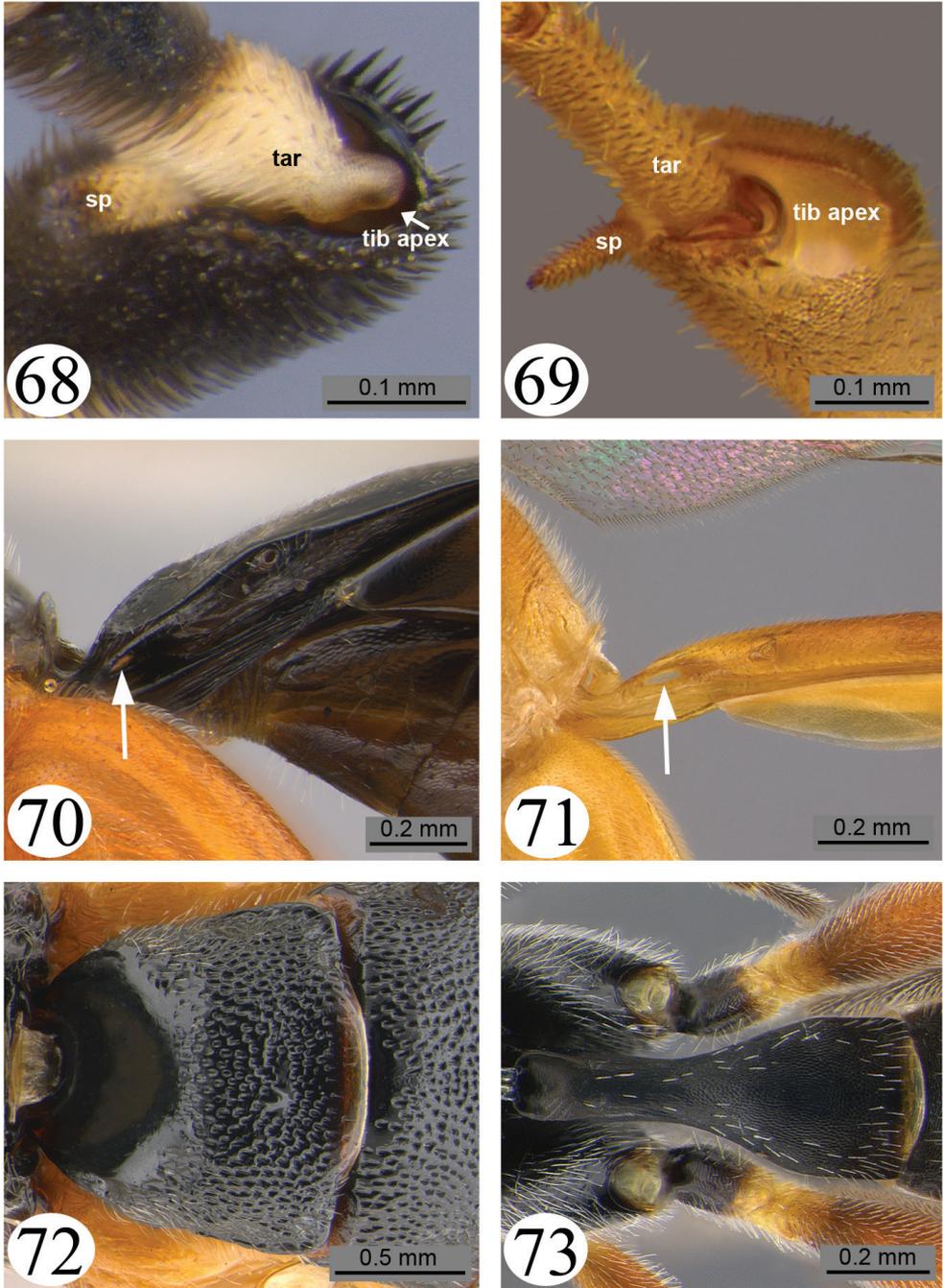


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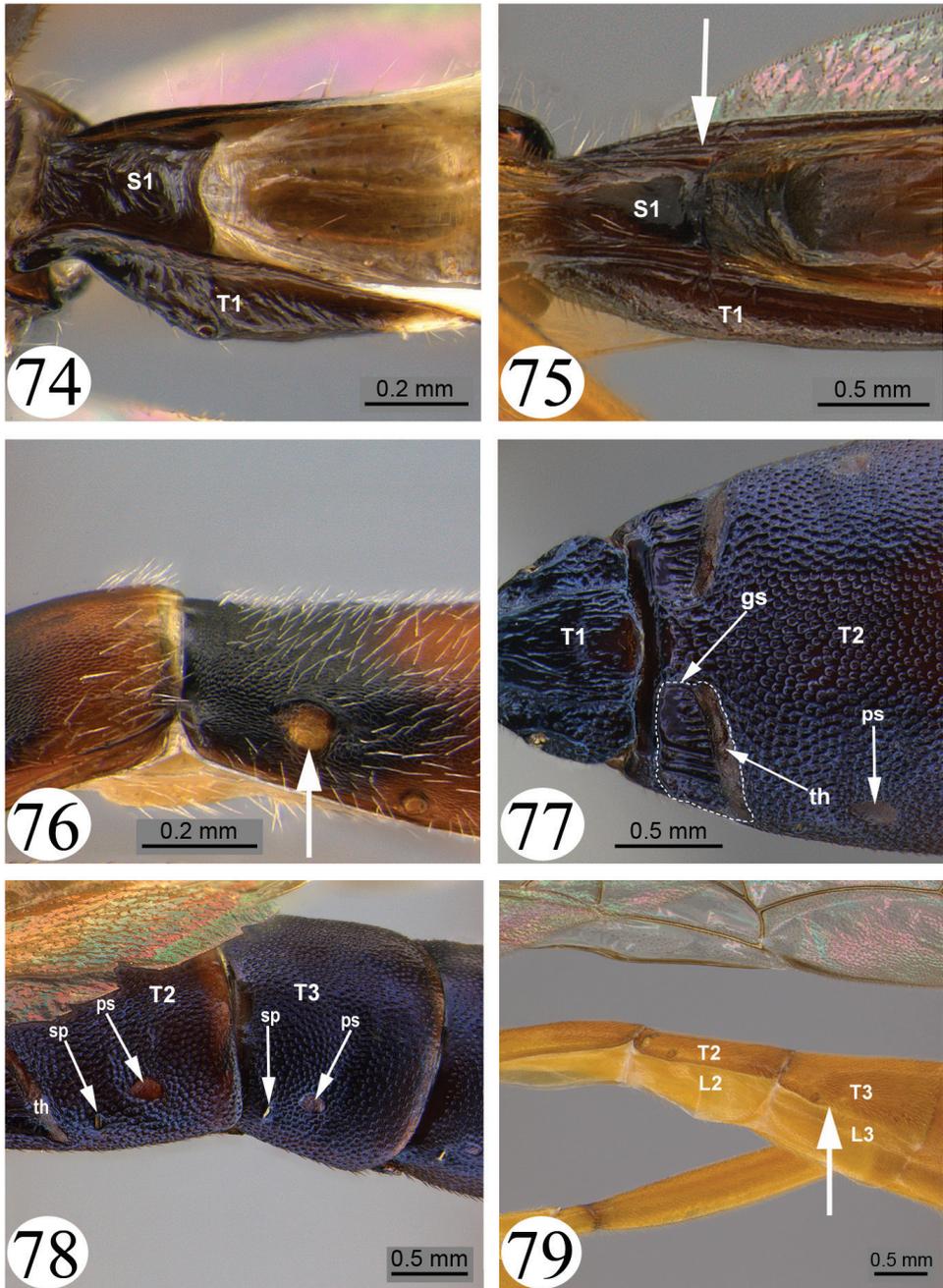


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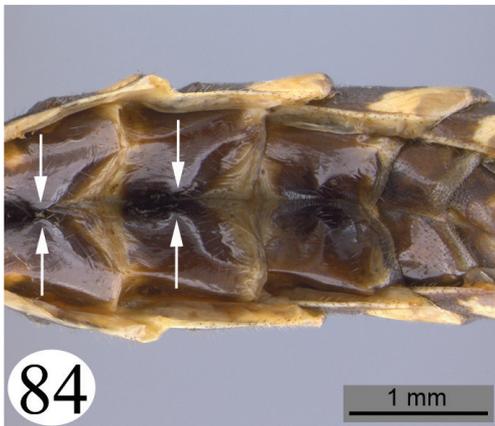
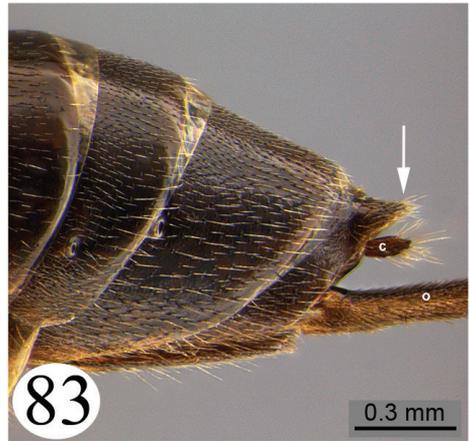
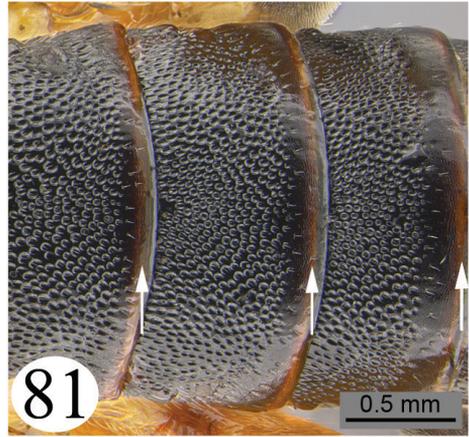
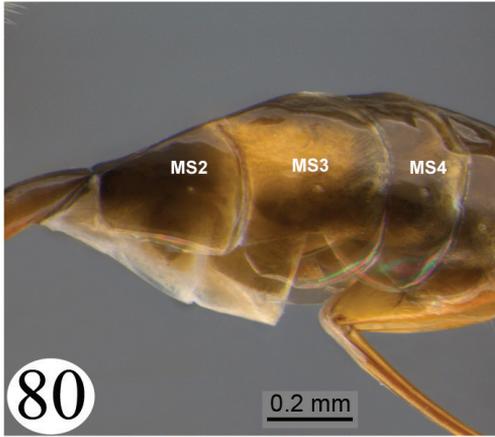
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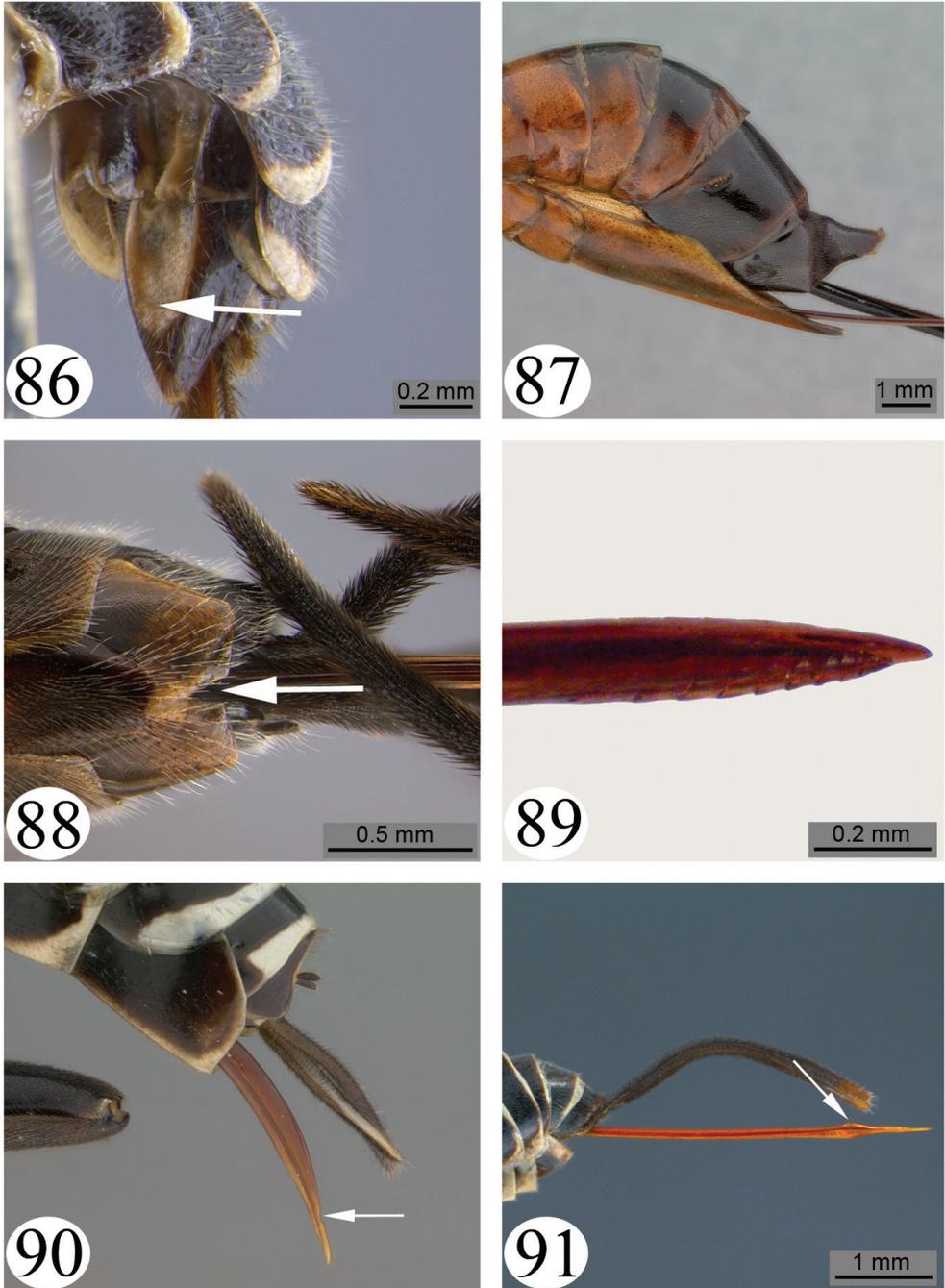
Figures 68–73. 68–69 Hind tibial apex, apical view. *sp* = spur, *tar* = tarsus, *tib apex* = tibial apex **68** *Polyblastus pedalis* (simple apex with sparse fringe of stout setae) **69** *Pedunculus* sp. (apex with apical face smooth and enlarged with thick fringe of fine setae) **70–71** Tergite 1 of metasoma, lateral view **70** *Phytodietus vulgaris* Arrow points to glymma **71** *Netelia* sp. Arrow points to deep glymma (sides of glymma separated medially by only a thin, translucent sclerite) **72–73** Tergite 1, dorsal view **72** *Pimpla aequalis* **73** *Campoletis sonorensis* (Cameron).



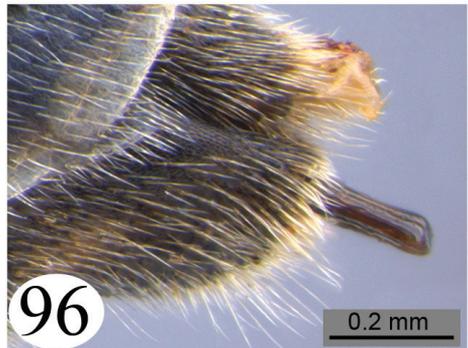
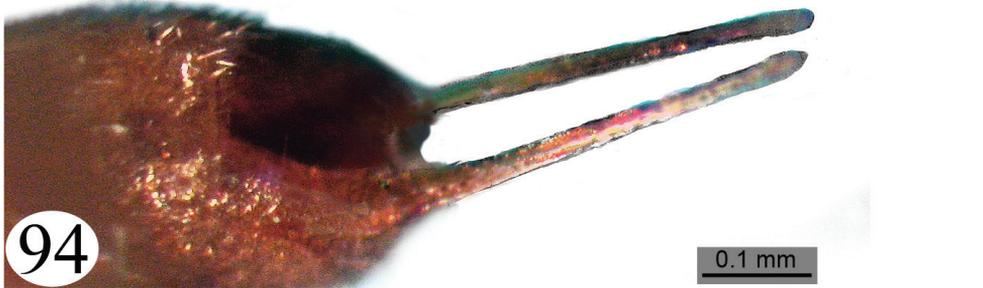
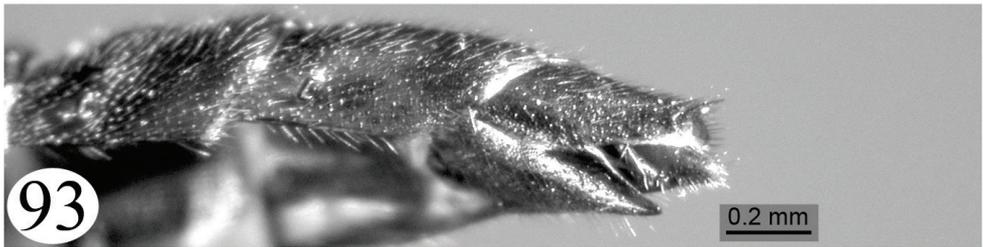
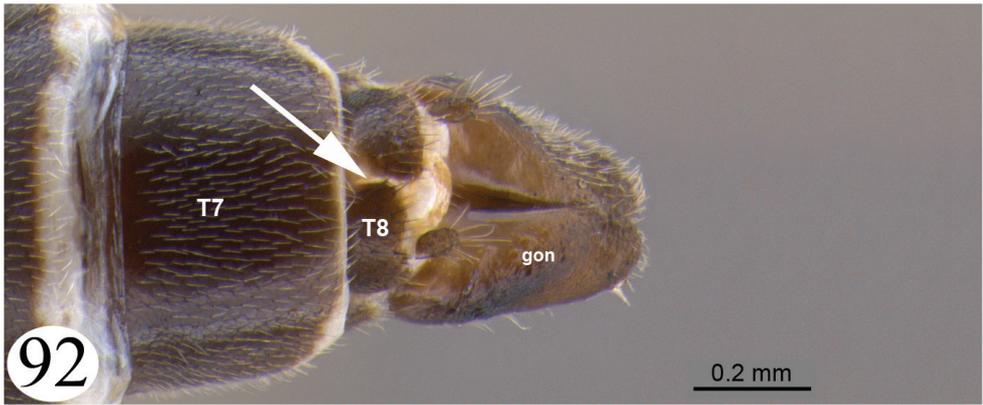
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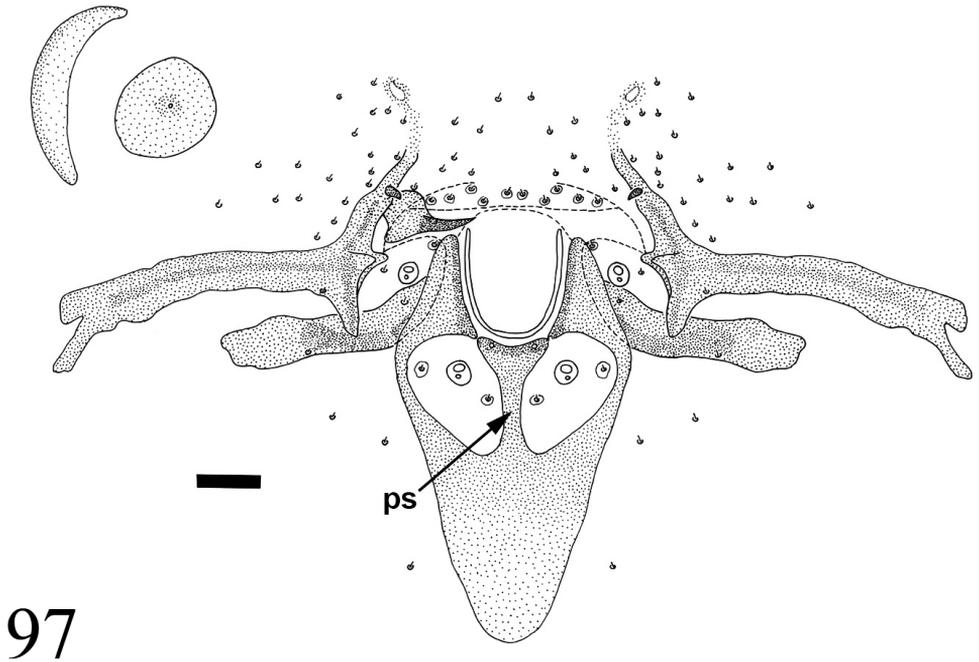
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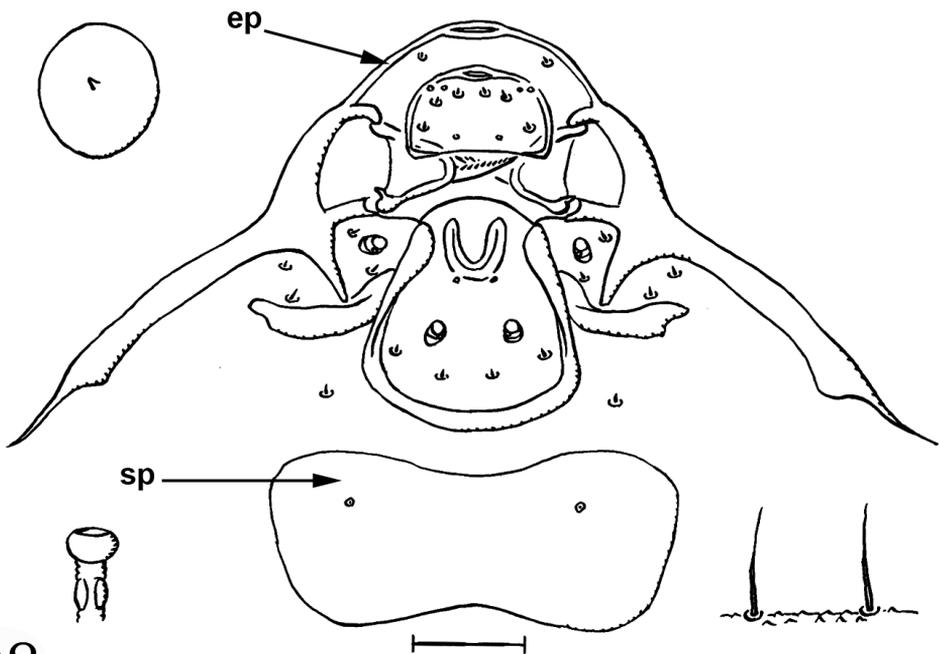
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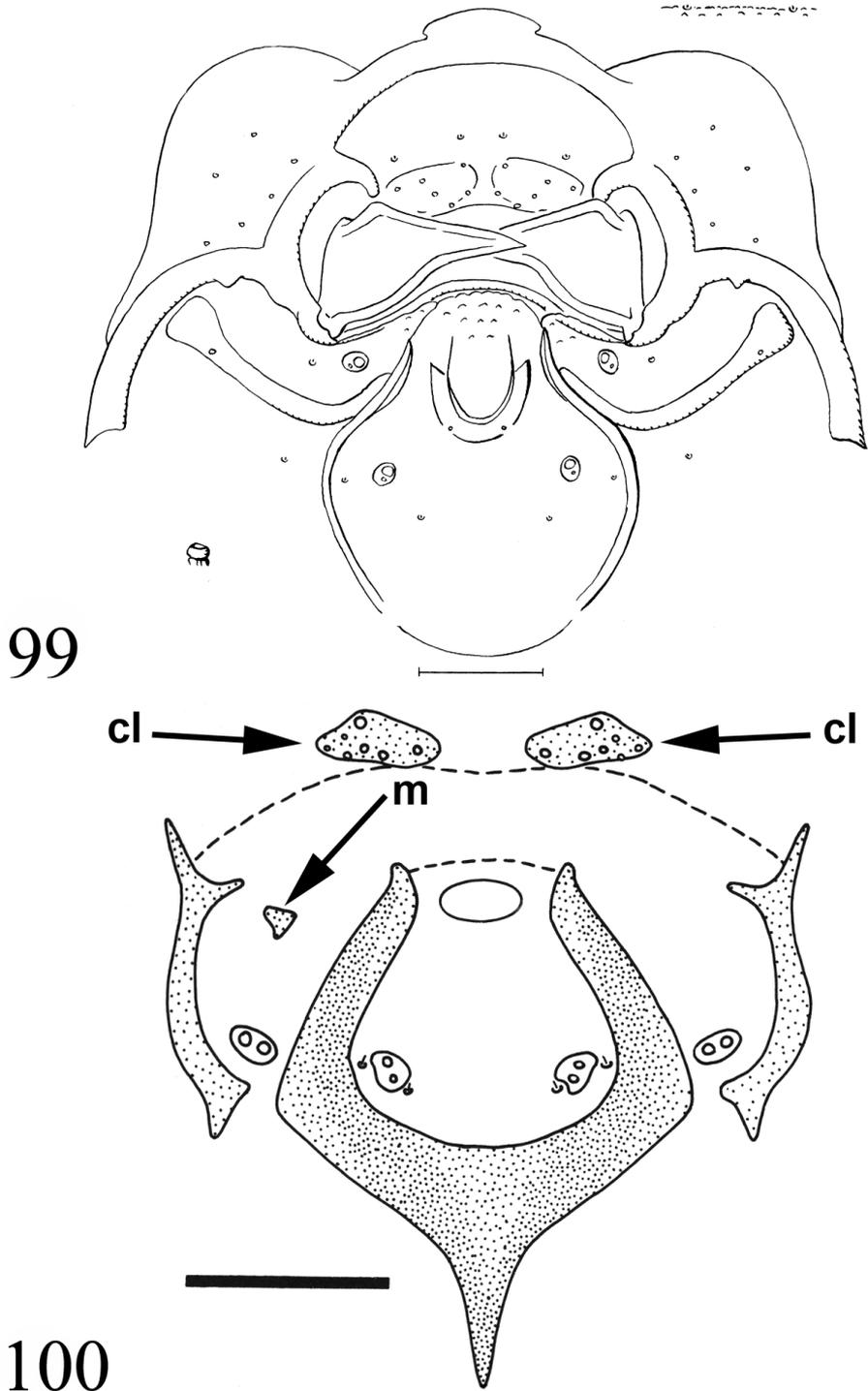


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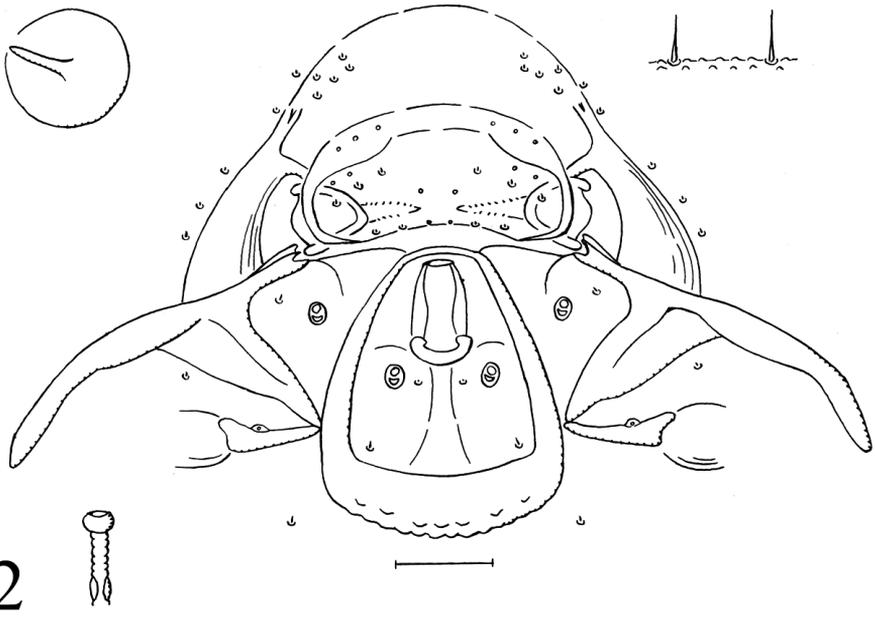
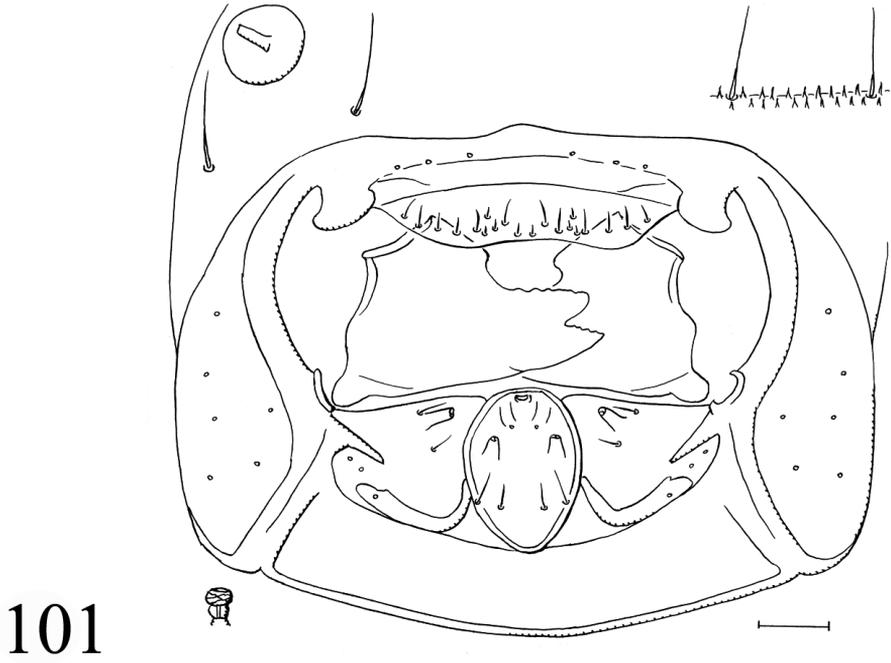


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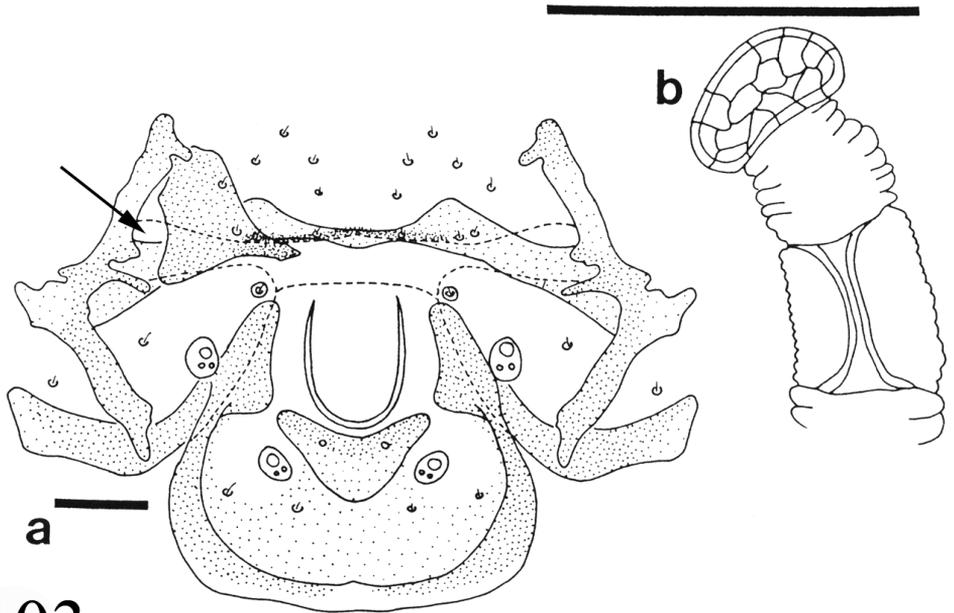
Figures 97–98. Cephalic sclerites of final larval instar **97** *Dusona* sp. (copied from Wahl 1990) *ps* = pre-labial sclerite **98** *Phytodietus polyzonias* Förster (copied from Short 1978) *ep* = epistomal band, *sp* = sclerotized plate ventral to labial sclerite.



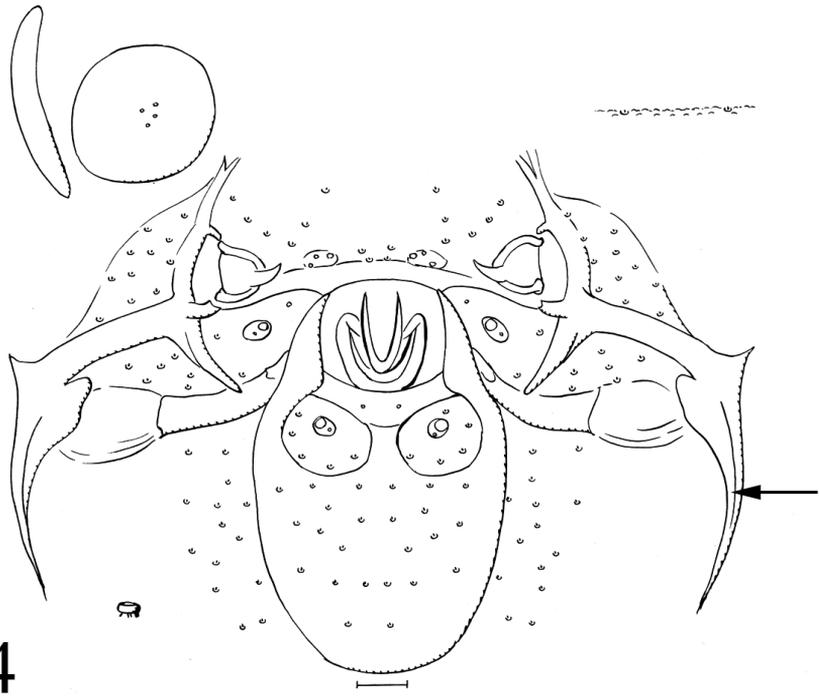
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Figures 101–102. Cephalic sclerites of final larval instar **101** *Poecilocryptus nigromaculatus* (copied from Short 1978) **102** *Dolichomitus irritator* (copied from Short 1978).

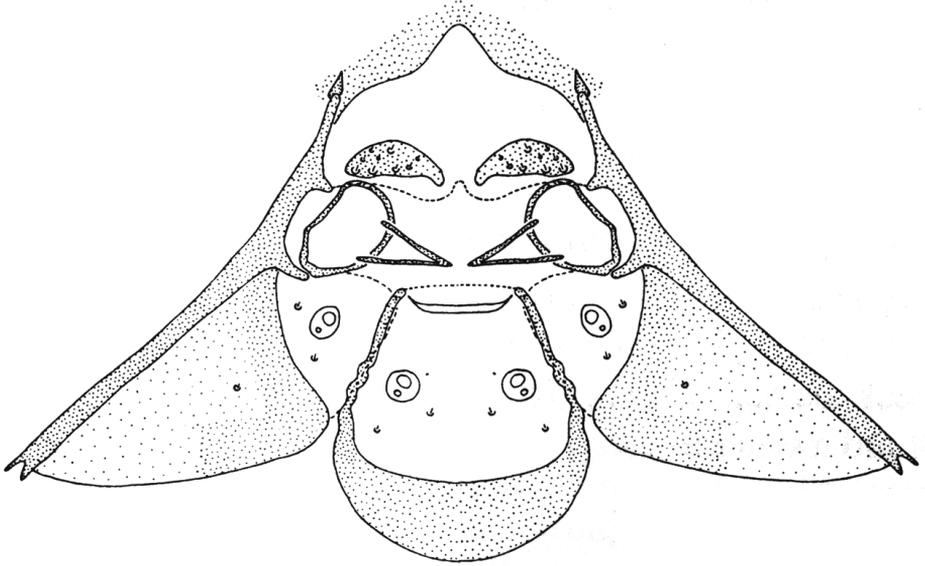


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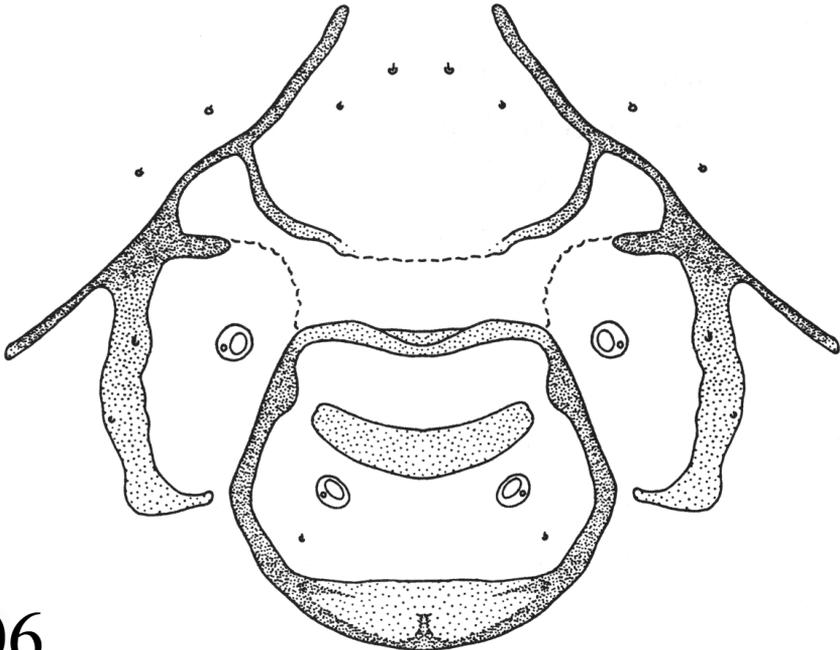


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Figures 103–104. Cephalic sclerites of final larval instar **103** *Lissonota occidentalis* (Cresson) (copied from Wahl 1988). Arrow points to lateral edge of lightly sclerotized band connecting posterior struts of inferior mandibular processes **104** *Enicospilus biharensis* Townes, Townes & Gupta (copied from Short 1978). Arrow points to ventral end of hypostoma.

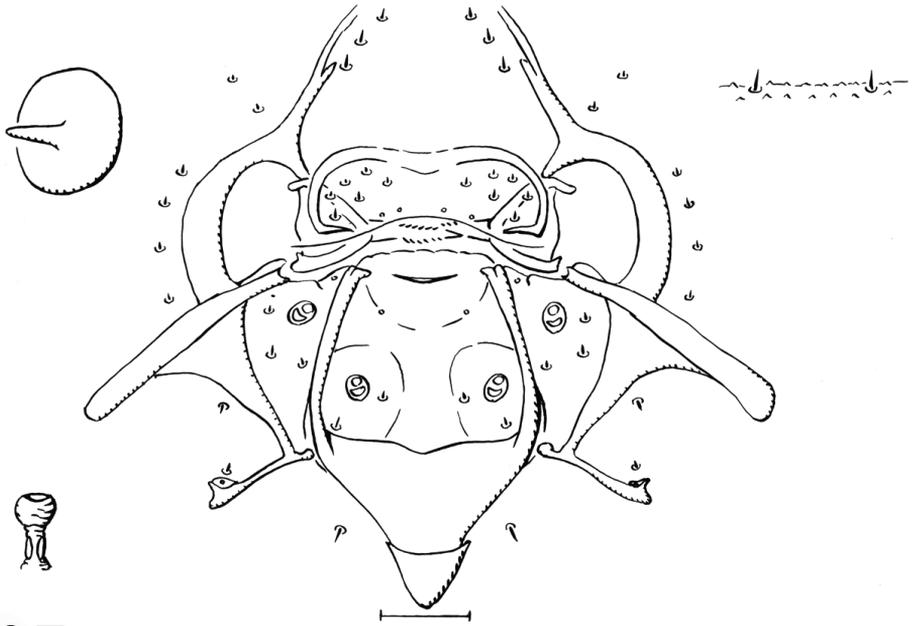


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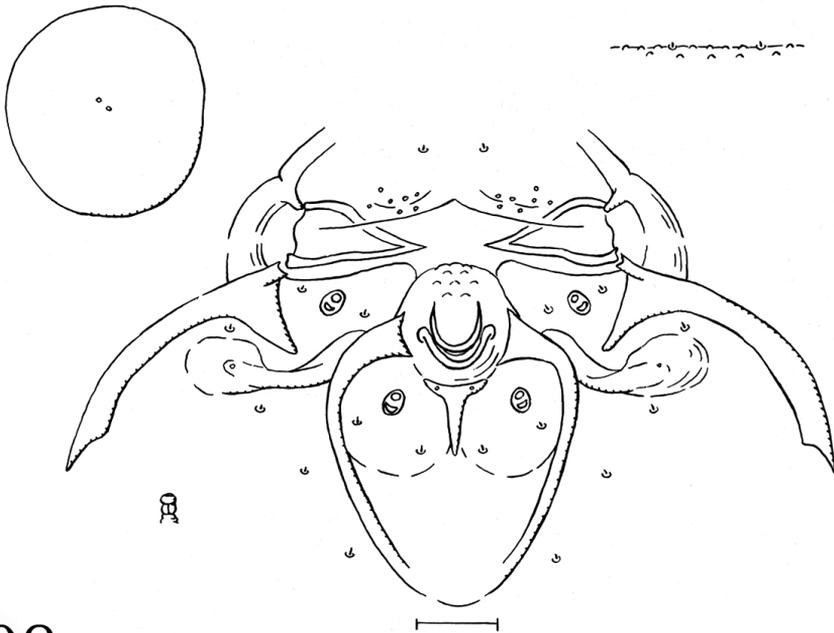


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Figures 105–106. Cephalic sclerites of final larval instar **105** *Spilopteron* sp. (modified from Wahl 1990)
106 *Megastylus* sp. (modified from Wahl 1990).

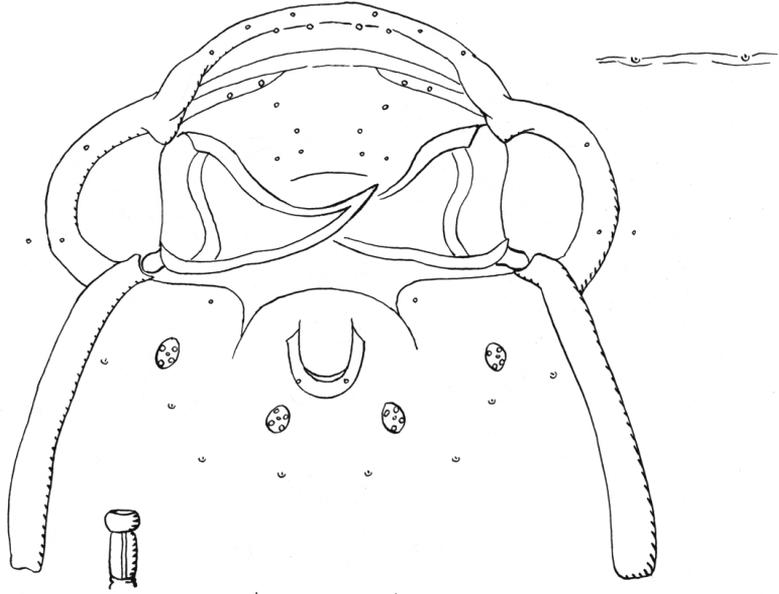


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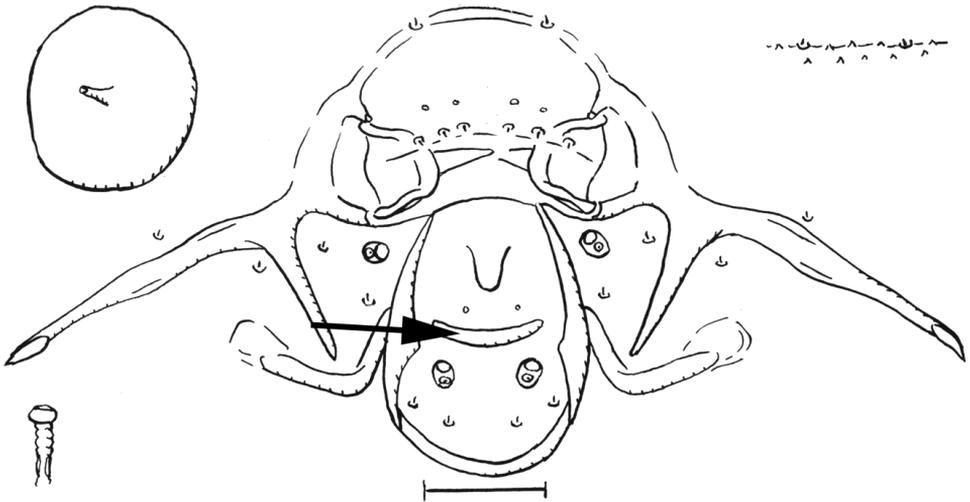


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Figures 107–108. Cephalic sclerites of final larval instar **107** *Neoxorides borealis* (copied from Short 1978) **108** *Rhimphoctona aldrichi* (Davis) (copied from Short 1978).

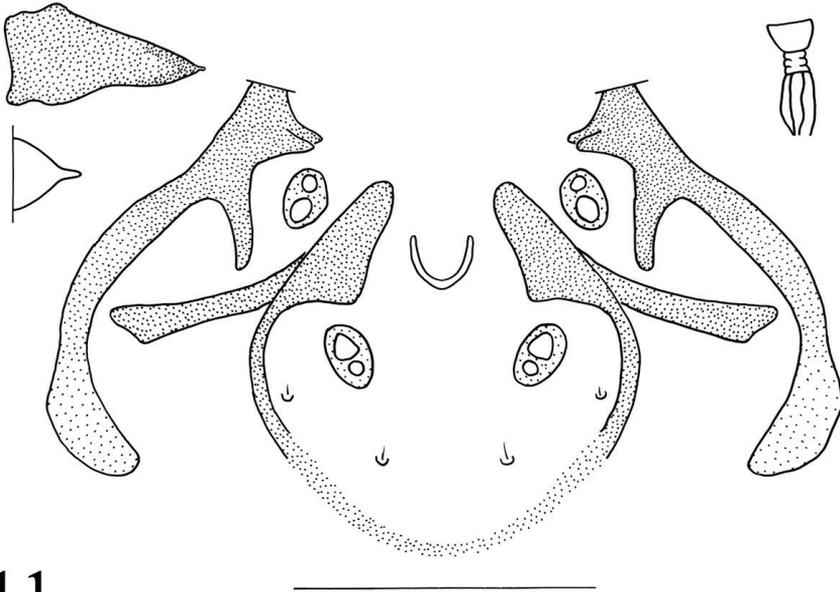


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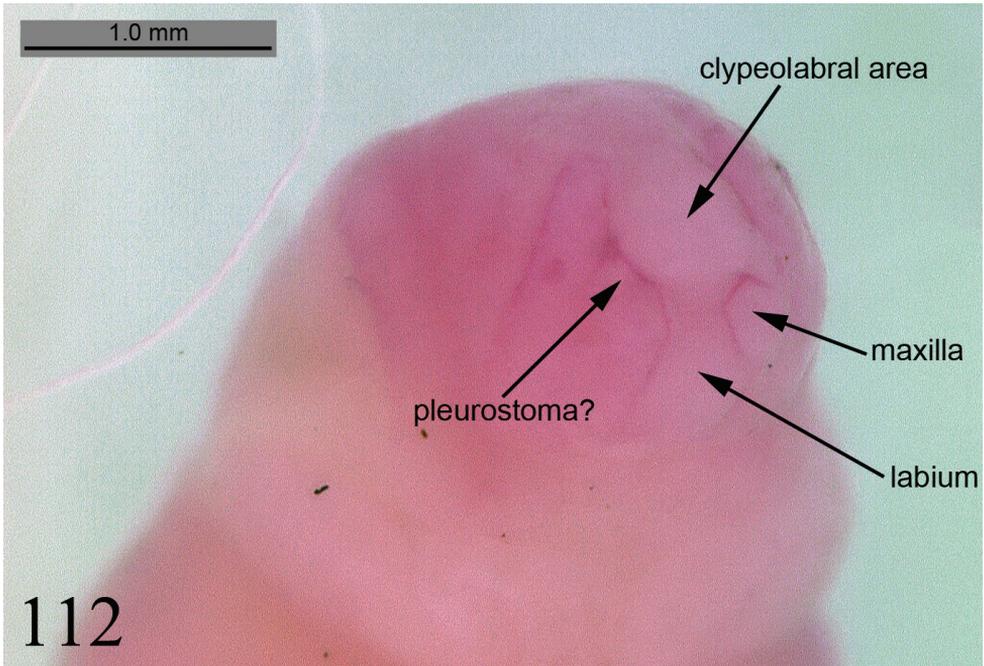


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Figures 109–110. Cephalic sclerites of final larval instar **109** *Phaeogenes hebrus* (copied from Short 1978) **110** *Euceros serricornis* (Haliday) (copied from Short 1978). Arrow points to prelabial sclerite.

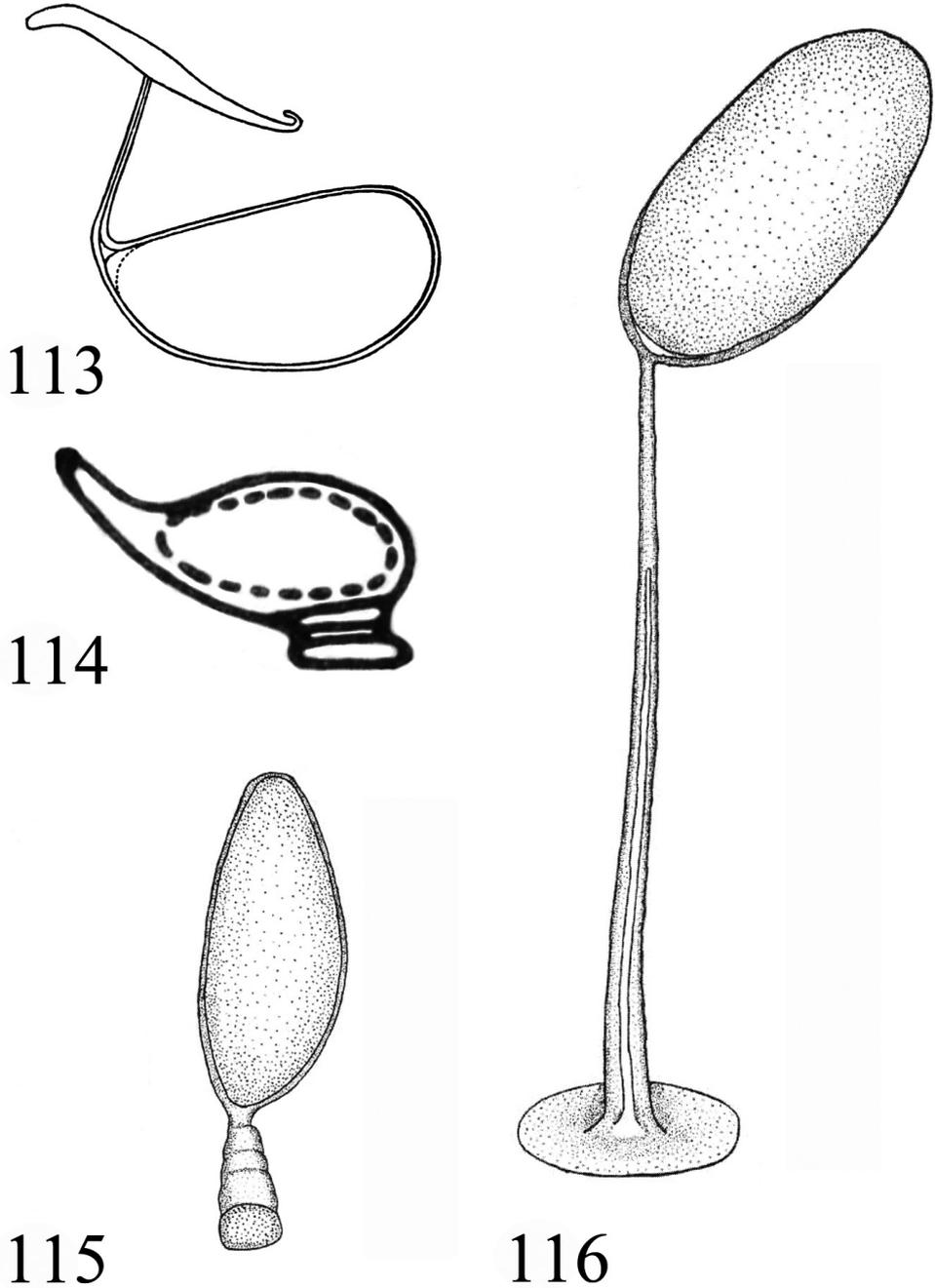


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Figures 111–112. 111 Cephalic sclerites of final larval instar, *Phrudus* sp. Figures in upper left corner is whole mandible (upper) and close-up of apex of mandible (lower). Scale bar: 0.1 mm. Mandible and spiracle not same scale as main figure (spiracle is 27 μ m in length) 112 Final larval instar, anterior of whole larva, *Collyria catoptron*, lateroventral view of head and thorax (stained with acid fuschin).



Figures 113–116. **113** Mature egg of *Ctenochira sanguinatoria* (Ratzeburg) (re-drawn after Kasparyan 1973) **114** Ovarian egg of *Therion* sp. egg (re-drawn after Iwata 1960) **115** Mature ovarian egg of *Euceros frigidus* Cresson (copied from Tripp 1961) **116** Egg of *Euceros frigidus* following oviposition (copied from Tripp 1961).

Morphological and biological characters only

The parsimony analysis using only the 141 morphological and biological characters produced 3872 equally parsimonious trees of 1527 steps (C.I. = 0.15, R.I. = 0.60). The strict consensus had 75 nodes collapsed (Fig. 118). Despite the lack of resolution in the “middle” of the tree, 14 of the 29 groupings considered in Table 3 were recovered as monophyletic in this analysis. This number did not include any of the three major subfamily groupings, which illustrates that our morphological data set was not good at resolving old divergences, but was relatively successful at supporting the monophyly of subfamilies. Agriotypinae (*Agriotypus armatus* Curtis) was always the sister group of all other Ichneumonidae. This analysis provided support for six subfamilies that were not monophyletic in the parsimony analysis with all characters (i.e., Acaenitinae, Banchinae, Mesochorinae, Metopiinae, Orthocentrinae and Xoridinae), but overall, it was much less well-resolved than the total-evidence parsimony analysis.

Molecular characters only

The parsimony analysis with molecular characters found 104 trees of 8126 steps (C.I. = 0.16, R.I. of 0.42). Ten nodes collapsed in the strict consensus cladogram (Fig. 119). Lycorininae (*Lycorina glaucomata* Cushman) was sister to all other Ichneumonidae, followed by *Neorhacodes enslini* (Ruschka) (Neorhacodinae), *Phytodietus vulgaris* Cresson and then *Netelia* sp. (both Tryphoninae). Nine of the 29 groupings in Table 3 were supported (including Pimpliformes) as well as 3 others that would be monophyletic if equivocally classified taxa were included or excluded (Banchinae, Metopiinae, and the *Phrudus* group of genera). Apart from the base of the tree, the overall topology more closely resembled the total-evidence parsimony analysis (Fig. 117), rather than the parsimony analysis with only morphological and biological characters (Fig. 118). This implies that the molecular data contributed more signal to the “middle” nodes of the tree than the morphological data.

Bayesian analysis

Total-evidence

The total-evidence Bayesian analysis majority credibility tree is shown in Figure 120. The topology at the base of the tree differed from the total-evidence parsimony analysis (Fig. 117). (Xoridinae was not sister to all other Ichneumonidae and Orthopelmatinae was not sister to all species except the xoridines). Instead, the Bayesian tree was similar to the parsimony analysis with only molecular characters (Fig. 119), in that its base had a grade of taxa: *Neorhacodes enslini* + (*Netelia* sp. + *Phytodietus vulgaris*) + (*Lycorina glaucomata* + *Idiogramma longicauda* (Cushman) + the remaining Tryphoninae). Apart from the base of the tree, there were some similarities between the parsimony and Bayesian total-evidence analyses. For the Bayesian analysis, 11 of the 29 groupings in Table 3 were unequivocally supported (BPP = 100) as well as 5 others (Banchinae,

Table 3. Comparison of the monophyly of selected taxa with different phylogenetic analyses and data-sets. See footnotes and introduction for composition of selected taxa. “Yes” indicates that all taxa were supported in all equally parsimonious trees or had a support value of 100 in the Bayesian majority credibility tree. “No” indicates lack of monophyly in at least one most parsimonious tree or a support value of less than 100 in the Bayesian analysis. Pars. = parsimony; all = all characters; morph. = morphological and biological characters only; mol. = molecular characters only; Bayes = Bayesian analysis.

Taxon	Pars. (all)	Pars. (morph.)	Pars. (mol.)	Bayes (all)	Bayes (mol.)
Pimpliformes	Yes	No	Yes	Yes	Yes
Ichneumoniformes	No ¹	No	No	No	No
Ophioniformes	Yes	No	No	No	No
Acaenitinae	No	Yes	No	No	No
Anomaloninae	Yes	Yes	No	No	No
Banchinae	No ²	Yes	No ²	No ²	No ²
Campopleginae	Yes	No	Yes	Yes	Yes
Cremastrinae	Yes	Yes	Yes	Yes	Yes
Cryptinae	Yes	No	No	Yes	Yes
Ctenopelmatinae	No ³	No	No	No	No
Diplazontinae	Yes	Yes	Yes	Yes	Yes
Ichneumoninae	Yes	Yes	Yes ⁹	Yes	Yes ⁹
Labeninae	Yes	No	Yes	Yes	Yes
Mesochorinae	No ⁴	Yes	No	No ⁴	No ⁴
Metopiinae	No ⁵	Yes	No ⁵	No ⁵	No ⁵
Nesomesochorinae	Yes	No	No	No	No
Ophioninae	Yes	Yes	No	Yes	No
Orthocentrinae	No	Yes	No	No	No
<i>Phrudus</i> group	No ⁶	No	No ⁶	No ⁶	No ⁶
Phygadeuontinae	Yes	Yes	No	No	No
Pimplinae	No	No	No	No	No
Poemeniinae	Yes	Yes	Yes	Yes	No
Rhyssinae	Yes	Yes	Yes	Yes	Yes
Sisyrostolinae	No	No	No	No	No
Stilbopinae	No	No	No	No	No
Tersilochinae s.l.	No ⁷	No	No	No ⁷	No
Tersilochinae s.s.	Yes	Yes	Yes	Yes	Yes
Tryphoninae	No ⁸	No	No	No	No
Xoridinae	No	Yes	No	Yes	No

¹ Ichneumoniformes of Wahl (1993) ((Ichneumoninae including *Alomya*) + Cryptinae (including Phygadeuontinae) + Brachycyrtinae)) shared a common ancestor, but ancestor shared with *Clasis*, *Pedunculus*, Labeninae, *Agriotypus*, *Euceros*, *Adelognathus*, and *Microleptes* (this group called Ichneumoniformes s.l.).

² All Banchinae shared a common ancestor, but ancestor shared with *Notostilbops* (Stilbopinae).

³ All Ctenopelmatinae shared a common ancestor, but ancestor shared with *Hybrizon*, *Lycorina*, *Oxytorus*, and *Tatogaster* as well as *Chineater* (Mesochorinae) and *Scolomus* (Metopiinae).

⁴ All Mesochorinae shared a common ancestor except for *Chineater* (see ³, above).

⁵ All Metopiinae shared a common ancestor except for *Scolomus* (see ³, above).

⁶ *Phrudus* and *Peucobius* shared a common ancestor, but ancestor shared with *Erythrodoilius* (Sisyrostolinae).

⁷ All Tersilochinae and Sisyrostolinae shared a common ancestor (albeit with very low support).

⁸ All Tryphoninae shared a common ancestor, but ancestor shared with *Neorhacodes* (Neorhacodinae).

⁹ All Ichneumoninae shared a common ancestor, but *Alomya* was not sister group to this grouping.

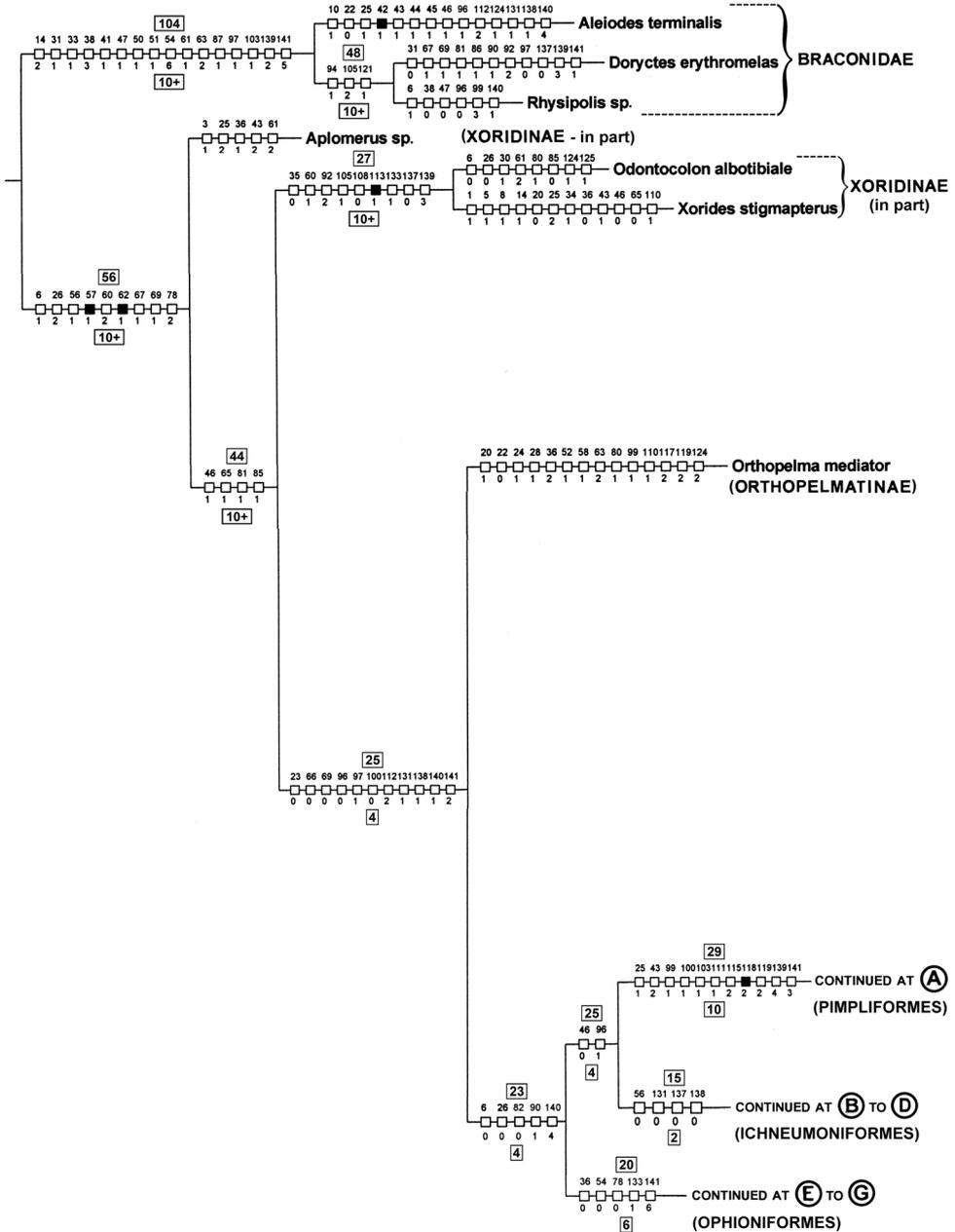


Figure 117. Part 1. Total-evidence parsimony analysis. Strict consensus cladogram (14 nodes collapse). Number of most parsimonious cladograms = 1728, length = 9917, CI = 0.15, RI = 0.44. Morphological characters optimized on tree using ACCTRAN. Open boxes are homoplasiously derived character states. Closed boxes are uniquely derived character states. Small numbers above boxes are character numbers. Small numbers below boxes are character states. Large numbers in squares above characters are total number of supporting characters (morphological and molecular). Large numbers in squares below characters are Bremer support values. Taxon names reflect classification prior to study (taxa with asterisks after name are formally re-classified in current study). “A” continued on part 2 of Fig. 117; “B–D” continued on part 3; “E–G” continued on part 4.

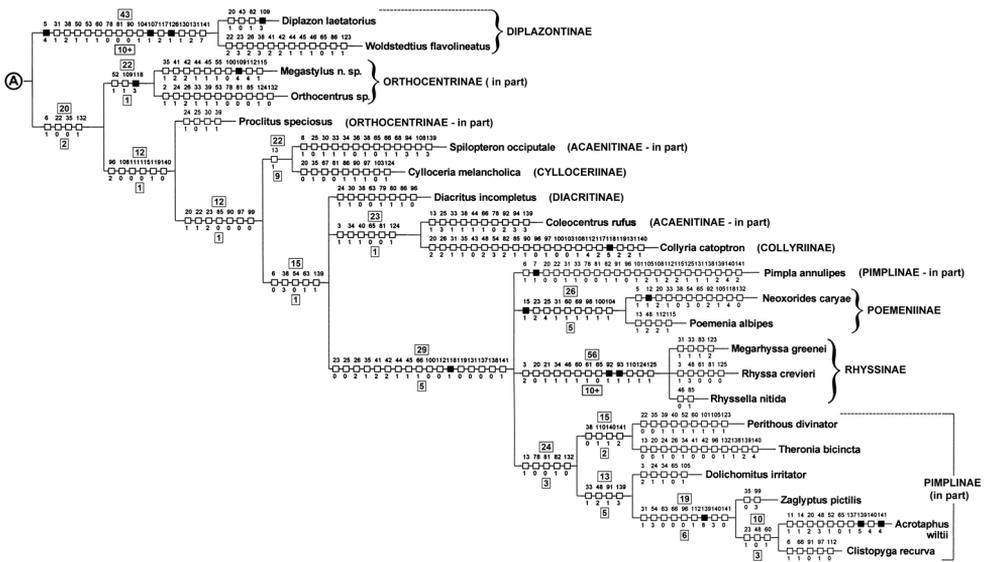


Figure 117. Part 2. Total-evidence parsimony analysis strict consensus cladogram continued from part 1 of Fig. 117. Pimpliformes group of subfamilies. See Fig. 117, part 1 figure heading for description of figure.

Mesochorinae, Metopiinae, the *Phrudus* group and Tersilochinae s.l.) that would be monophyletic with the inclusion or exclusion of equivocally classified taxa. Pimpliformes was unequivocally supported, but not Ichneumoniformes (either strictly or broadly defined) or Ophioniformes. Neither was there support for Pimpliformes + Ichneumoniformes s.l. This was because Labeninae was recovered as sister group to Pimpliformes + Ichneumoniformes s.l. The remainder of the subfamilies in Ichneumoniformes s.l., did group with Pimpliformes with a high support value (BPP = 98). In general, the basal nodes of the tree were weakly supported (BPP < 90), suggesting that more data are required for these regions of the tree.

Molecular characters only

Similar to the total-evidence Bayesian analysis and the parsimony analysis with only molecular characters, the base of the tree for the Bayesian analysis with only molecular characters (Fig. 121) consisted of a grade of Ophioniformes species (Neorhacodinae, Lycorininae and Tryphoninae). The analysis found unequivocal support for 8 of the 29 groupings in Table 3, including Pimpliformes. Banchinae, Mesochorinae, Metopiinae and the *Phrudus* group would also be supported with inclusion or exclusion of problematic taxa. Ichneumoniformes s.l. except for Labeninae was moderately well supported (BPP = 95) and was unequivocally the sister group of Pimpliformes. Labeninae was the sister of these two groupings with a much higher support value (BPP = 99) than the total-evidence Bayesian analysis (BPP = 66) (Fig. 120), suggesting that the morphological and molecular data were conflicting with respect to the placement of Labeninae.

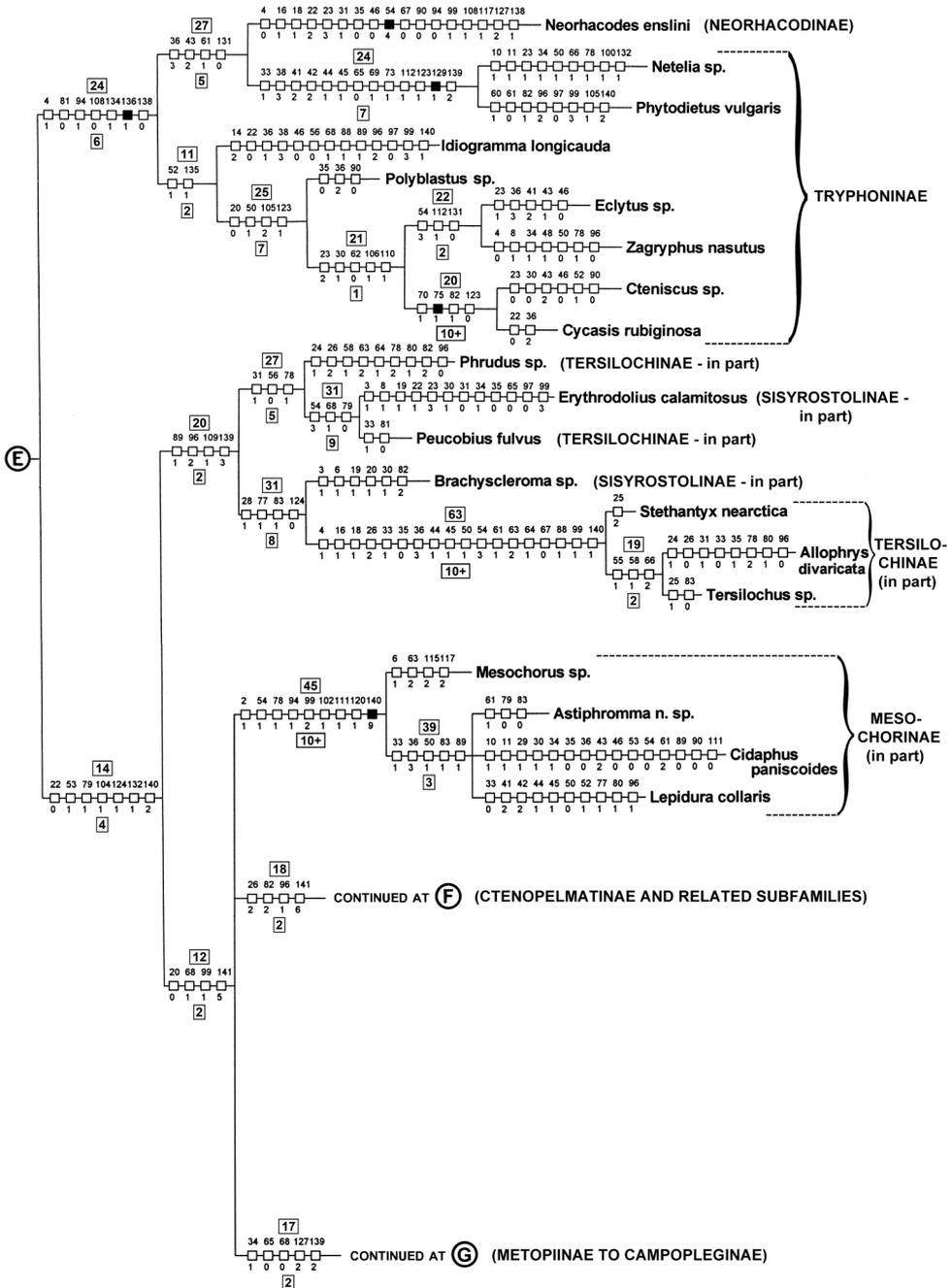


Figure 117. Part 4. Total-evidence parsimony analysis strict consensus cladogram continued from part 1 of Fig. 117. Ophonionformes group of subfamilies (base of clade). See Fig. 117, part 1 figure heading for description of figure. “F” continued on part 5 of Fig. 117; “G” continued on part 6 of Fig. 117.

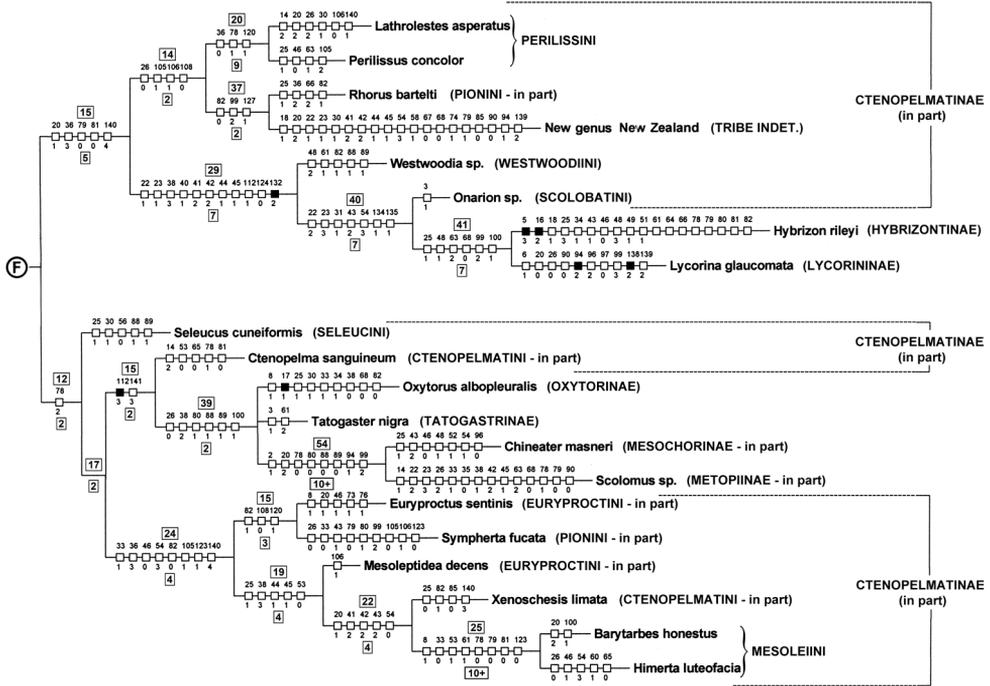


Figure 117. Part 5. Total-evidence parsimony analysis strict consensus cladogram continued from part 4 of Fig. 117. Ctenopelmatinae and related subfamilies. See Fig. 117, part 1 figure heading for description of figure.

Support/relationships of taxa

Ichneumonidae

It was not the purpose of this study to examine relationships outside of Ichneumonidae, therefore only minimal outgroup sampling was used; however, all analyses did recover a monophyletic Ichneumonidae (Figs 117–121). In the total-evidence parsimony analysis, Ichneumonidae was supported by a Bremer support of greater than 10 steps and 56 synapomorphies, 9 of which were morphological, including two that were uniquely derived: character 57, state 1: fore wing with antero-medial flexion line basally with the anterior fold running posterior to vein M (basal vein of areolet without a bulla); and character 62, state 1: hind wing vein *Ir-m* opposite or apical to separation of veins *R1* and *R*_s (Fig. 4 compared to Fig. 49 for both of these characters).

Sister group to all other Ichneumonidae

The following taxa were sister group to all other Ichneumonidae depending on the analysis:

Aplomerus sp. (Xoridinae): total-evidence parsimony analysis (Fig. 117);

Agriotypus armatus (Agriotypinae): morphology-only parsimony analysis (Fig. 118);

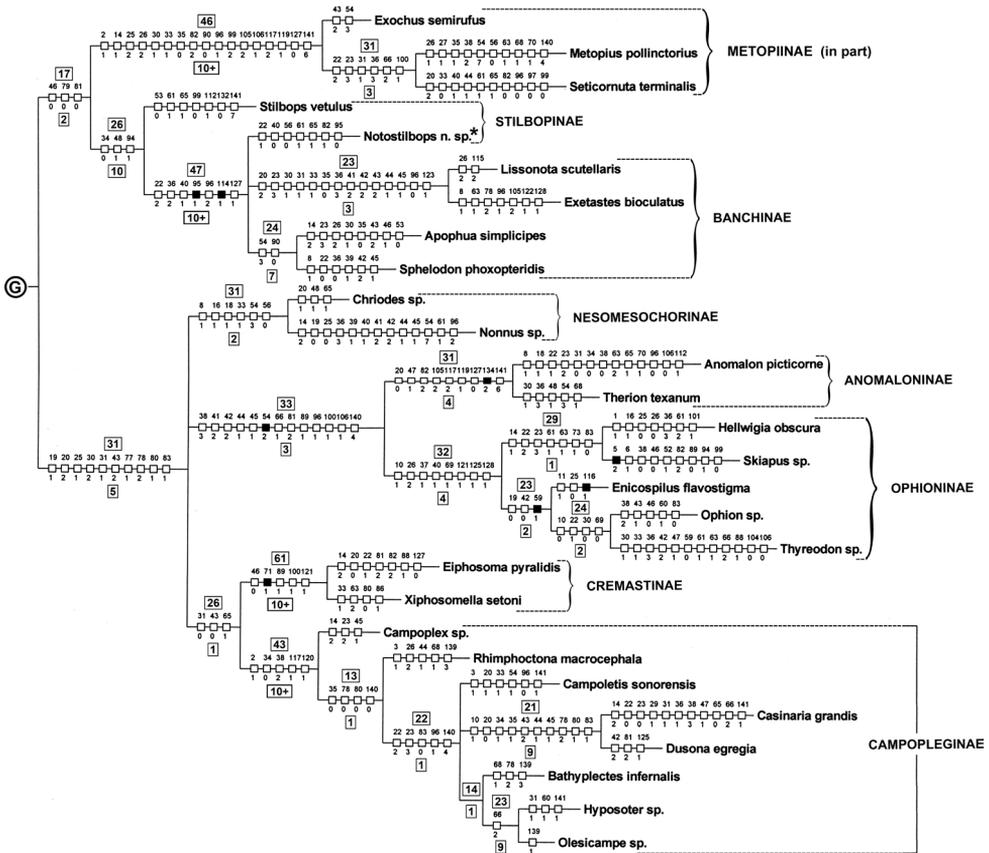


Figure 117. Part 6. Total-evidence parsimony analysis strict consensus cladogram continued from part 4 of Fig. 117. Metopiinae to Campopleginae. See Fig. 117, part 1 figure heading for description of figure.

Lycorina glaucomata (Lycoriniinae): molecular-only parsimony analysis (Fig. 119);
Neorhacodes enslini (Neorhacodinae): Bayesian analyses (Figs 120–121).

Our total-evidence parsimony analysis found the three Xoridinae species at the base of Ichneumonidae; however, they were not monophyletic with *Aplomerus* Provancher sister group to all other ichneumonids and (*Odontocolon* Cushman + *Xorides* Latreille) sister to all the rest (Fig. 117). In contrast, Xoridinae was monophyletic in the morphology-only parsimony analysis (Fig. 118) and both Bayesian analyses (Figs 120–121), albeit not as sister to the rest of Ichneumonidae. The biology of Xoridinae (ectoparasitoids of wood-boring beetles) is consistent with the hypotheses of Handlirsch (1907) and Gauld (1988a) with respect to the evolution of parasitoidism beginning with idiobiont ectoparasitoids in concealed substrates.

In our morphological parsimony analysis, the clade comprising all ichneumonids except *Agriotypus armatus* was supported by 11 synapomorphies, of which one was uniquely derived: character 87(0) (T2 and T3 separate, with flexion line allowing move-

ment) (Fig. 78). The Bremer support value was only 1. In all of our other analyses, Agriotypinae was placed within Ichneumonidae, with the fusion of T2 and T3 evolving in parallel in Braconidae and Agriotypinae. Agriotypinae are idiobiont ectoparasitoids of pupal and pre-pupal Trichoptera in fast-running streams (Bennett 2001).

The evidence that Lycorinae is sister group to all other ichneumonids is based on 36 uniquely derived molecular substitutions that support the clade comprising all ichneumonids except *Lycorina glaucomata* in the molecular parsimony analysis (Fig. 119). Among our five analyses, the placement of Lycorinae was one of the least stable of any taxon. The total-evidence parsimony analysis placed *L. glaucomata* within the Ctenopelmatinae and relatives clade as sister to Hybrizontinae (see section on Hybrizontinae for details on support). In the two Bayesian analyses, it was placed within a grade near the bottom of the cladogram along with *Neorhacodes enslini* (Neorhacodinae) and various species of Tryphoninae (Figs 120–121).

The biology of *Lycorina* is not completely known, but species for which oviposition and development have been observed are koinobionts (Coronado-Rivera et al. 2004) that oviposit in the anus of Lepidoptera larvae and complete development feeding externally on the host and pupating inside the host cocoon (Shaw 2004) (our character 138, state 2).

Neorhacodinae was sister group to all other Ichneumonidae in both Bayesian analyses on the basis of posterior probabilities of 100 supporting the grouping comprised of all ichneumonids except *Neorhacodes enslini* (Figs 120–121). The parsimony analysis with only molecular characters placed *N. enslini* close to its placement in the Bayesian analyses, as the sister taxon to all Ichneumonidae except *Lycorina glaucomata* (Lycorinae) (part 1 of Fig. 119). Conversely, the total-evidence parsimony analysis placed *N. enslini* within Tryphoninae (as sister to Phytodietini) (part 4 of Fig. 117). The biology of Neorhacodinae is not completely known. *Neorhacodes* spp. have been reared from nests of aculeate Hymenoptera (Horstmann 1968; Danks 1971) and are probably endoparasitoids (Wahl 1993c), but it is not clear whether they are idiobionts or koinobionts.

In terms of previous studies, Quicke et al. (1999) using 28S D2–D3 sequence data analyzed with parsimony for a limited taxon sampling of Ichneumonoidea found that Xoridinae was sister group to all other Ichneumonidae. Similarly, the analyses of Klopstein et al. (2019) using transcriptomes from 6 braconids and 19 ichneumonids found that *Xorides praecatorius* (Fabricius) was sister to all other ichneumonids and this same placement was also found in all of their anchored enrichment analyses of 84 taxa, including 10 non-ichneumonid outgroups. Quicke (2015) summarized his “best-guess” by placing both Xoridinae and Labeninae unresolved as sister taxa to all other Ichneumonidae, and this arrangement was also presented by Broad et al. (2018). Apart from Xoridinae and Labeninae, Agriotypinae (*Agriotypus* Curtis) has previously been accorded family group status within Ichneumonoidea (e.g., Ashmead 1900) which could be consistent with a sister group relationship with all other Ichneumonidae, although all recent studies have concluded that it belongs within Ichneumonidae and most likely as part of Ichneumoniformes sensu lato (Quicke et al. 2009; Santos 2017). Similarly, Hybrizontinae (*Hybrizon* Fallén and two fossil genera) has been given family group status within Ichneumonoidea (e.g., Marsh 1989), but more recent studies

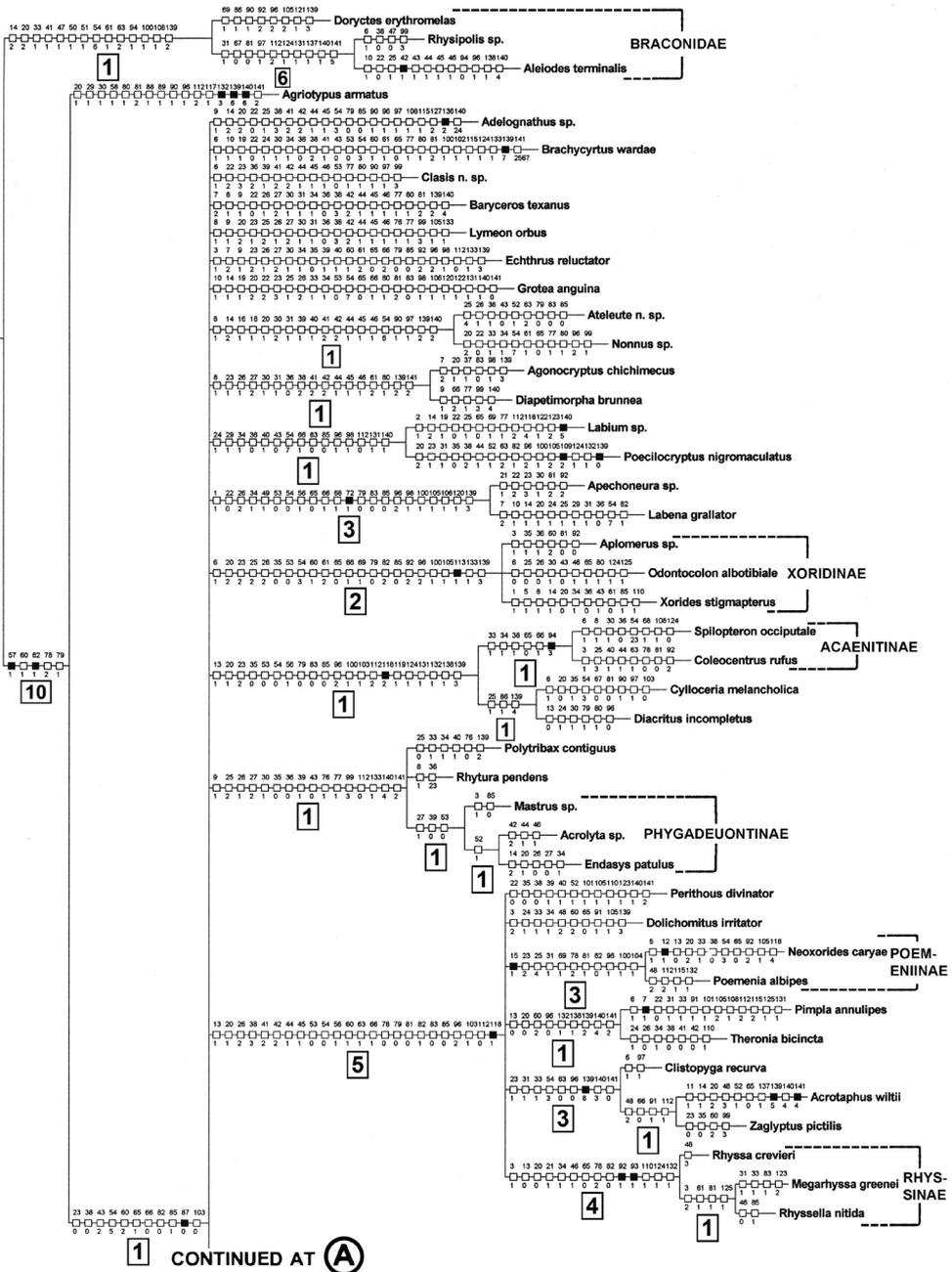


Figure 118. Part 1. Parsimony analysis (morphological and biological characters only: Chs 1-141). Strict consensus cladogram (75 nodes collapse). Characters optimized on tree using ACCTRAN. Number of most parsimonious cladograms = 3872, length = 1527, CI = 0.15, RI = 0.60. See Figure 117 figure heading for description of character support. Taxon names reflect classification prior to study (taxa with asterisks after name are formally re-classified in current study). "A" continued on part 2 of Fig. 118.



Figure 118. Part 3. Parsimony analysis (morphological and biological characters only) strict consensus cladogram continued from part 2 of Fig. 118. See Fig. 118, part 1 figure heading for description of figure.

place it within Ichneumonidae and more specifically, within Ophioniformes (Quicke et al. 2009, Broad et al. 2018). There was no evidence in the current study that Hybrizontinae was sister group to the rest of Ichneumonidae. Neorhacodinae (currently comprised of *Neorhacodes* Hedicke, *Romaniella* Cushman and *Eremura* Kasparyan) has been classified as a subfamily in both Ichneumonidae (e.g. Townes 1969) and Braconidae (Fahringer 1936), but it has never been given family group status within Ichneumonoidea, nor has it ever been suggested that it is the sister group of all other Ichneumonidae. This is also the case for Lycoriniinae. Both of these taxa have most recently been placed within Ichneumonidae and, more specifically, within Ophioniformes (Quicke et al. 2009; Broad et al. 2018). In summary, the only previously hypothesized sister group to all other Ichneumonidae that was supported in the current study was Xoridinae, and the only analysis that supported this (total-evidence parsimony), did not recover the subfamily as monophyletic (Fig. 117). Future studies should include a greater number of outgroups from Braconidae and outside Ichneumonoidea, in order to examine this question.

Subfamily groupings

Ophioniformes

Ophioniformes (including Tryphoninae) was supported in the total-evidence parsimony analysis by 20 total characters, of which 5 were morphological: 36(0) anterior transverse carina of propodeum complete (Fig. 38); 54(0) areolet obliquely rhombic to subtriangular (Fig. 51); 78(0) glymma present and shallow (Fig. 5); 133(0) larval salivary orifice u-shaped (Fig. 7g); and 141(0) larval-pupal oviposition-emergence. The Bremer support value of this node was 6 steps (part 1 of Fig. 117). None of the other analyses supported Ophioniformes as monophyletic and in general, Ophioniformes species formed a grade leading to the Ichneumoniformes and Pimpliformes taxa (e.g., Bayesian total-evidence tree: part 1 of Fig. 120).

In terms of the arrangement within Ophioniformes in the total-evidence parsimony analysis, Tryphoninae (including *Neorhacodes enslini*) was sister to all other taxa (part 4 of Fig. 117), which was similar to the findings of Quicke et al. (2009), albeit the latter study had taxa of some other subfamilies clustering within Tryphoninae (i.e., Eucerotinae, Sisyrostolinae, Stilbopinae, but not Neorhacodinae). Our total-evidence parsimony analysis next found a grouping of Sisyrostolinae and Tersilochinae as sister to all remaining Ophioniformes, followed by a clade without resolution comprised of the following three groups: 1) Mesochorinae (except *Chineater masneri* Wahl) (part 4 of Fig. 117); 2) Ctenopelmatinae and related subfamilies (part 5 of Fig. 117); and 3) (Metopiinae + *Stilbops* + Banchinae including *Notostilbops*) + the higher Ophioniformes. Higher Ophioniformes was a clade of three groups with equivocal relationships among the equally parsimonious trees: Nesomesochorinae/ (Anomaloninae + Ophioninae)/ (Cremastinae + Campopleginae) (part 6 of Fig. 117). In the total-evidence parsimony analysis, higher Ophioniformes was moderately well supported by 31 synapomorphies, of which 10

were morphological (none uniquely derived) and a Bremer support of 5. The group was also quite well-supported in the total-evidence Bayesian analysis (BPP = 98).

The topology within Ophioniformes in the current total-evidence parsimony analysis is similar to that of Quicke et al. (2009), with the following major exceptions: 1) Orthopelmatinae and Microleptinae never belonged to Ophioniformes in our study (equivocal placement in Quicke et al. 2009, but within Ophioniformes in both of their presented cladograms); 2) Tersilochinae was associated with Sisyrastolinae as opposed to related to Ctenopelmatinae and Mesochorinae in Quicke et al. (2009); 3) Mesochorinae and Metopiinae were not paraphyletic with respect to Ctenopelmatinae in our analysis; 4) Ctenopelmatinae could be monophyletic based on our results with the inclusion of four small subfamilies (Hybrizontinae, Lycorininae, Oxytorinae and Tatogastrinae) and inclusion of two enigmatic genera—*Chineater* Wahl (Mesochorinae) and *Scolomus* Townes & Townes (Metopiinae); 5) Hybrizontinae clustered with the Ctenopelmatinae exemplars in our study as opposed to related to *Skiapus* Morley (Ophioninae) and Anomaloninae in Quicke et al. (2009).

The anchored enrichment study by Klopstein et al. (2019) included 12 exemplars of Ophioniformes with the following topology: Tryphoninae + (Banchinae + (Tersilochinae + (Mesochorinae + (Ctenopelmatinae + (Metopiinae + (Anomaloninae + (Cremastinae + (Ophioninae + Campopleginae)))))). The main similarities between the current total-evidence parsimony analysis and the results of Quicke et al. (2009) and Klopstein et al. (2019) are: 1) Tryphoninae is sister to the rest of Ophioniformes; 2) Anomaloninae, Cremastinae, Ophioninae and Campopleginae cluster together as part of the higher Ophioniformes. The placement of the other subfamilies differed somewhat between these three studies and will be discussed in the relevant subfamily sections in *Support/relationships of subfamilies* (below).

Pimpliformes

Pimpliformes was monophyletic in all analyses with the exception of parsimony using only morphological characters (Table 3). In the total-evidence parsimony analysis it was supported by 29 characters, of which 11 were morphological, including the uniquely derived character 118(2) (larval hypostomal spur fused to form a hypostomal-stipital plate) (part 1 of Fig. 117). The Bremer support value was 10 steps. Most previous analyses have also supported Pimpliformes using either morphological data (Wahl and Gauld 1998), sequence data (Belshaw et al. 1998; Klopstein et al. 2019) or combined morphology and sequence data (Quicke et al. 2009).

In the current study, the topology within Pimpliformes was equivocal, depending on the method of analysis. The total-evidence parsimony and molecular parsimony analyses recovered Diplazontinae as sister to all other taxa, followed by the orthocentrine genera (not clustering together) and the rest of the taxa (part 4 of Fig. 117, part 2 of Fig. 119). In contrast, the Bayesian total-evidence analysis placed the taxa in two separate clades: 1) the “higher Pimpliformes” of Quicke et al. (2009) = Pimplinae, Poemeniinae and Rhyssinae; and 2) all other exemplars (part 2 of Fig. 120). Higher Pimpliformes was strongly supported in the parsimony total-evidence analysis with

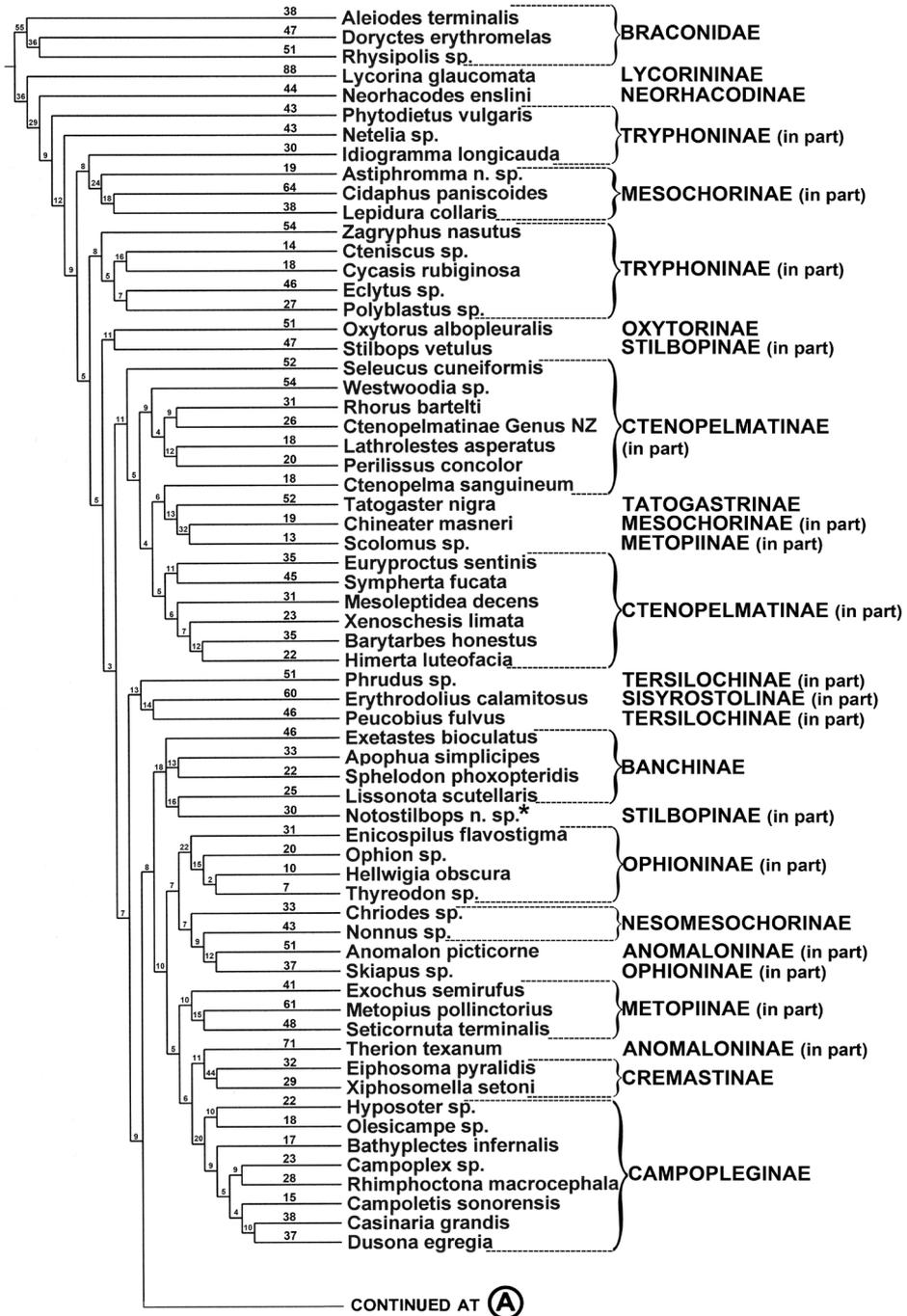


Figure 119. Part 1. Parsimony analysis (molecular characters only). Strict consensus cladogram (10 nodes collapse). Number of most parsimonious cladograms = 104, length = 8126, CI = 0.16, RI = 0.42. Numbers above branches are number of substitutions supporting each node or taxon. Taxon names reflect classification prior to study (taxa with asterisks after name are formally re-classified in current study). “A” continued on part 2 of Fig. 119.

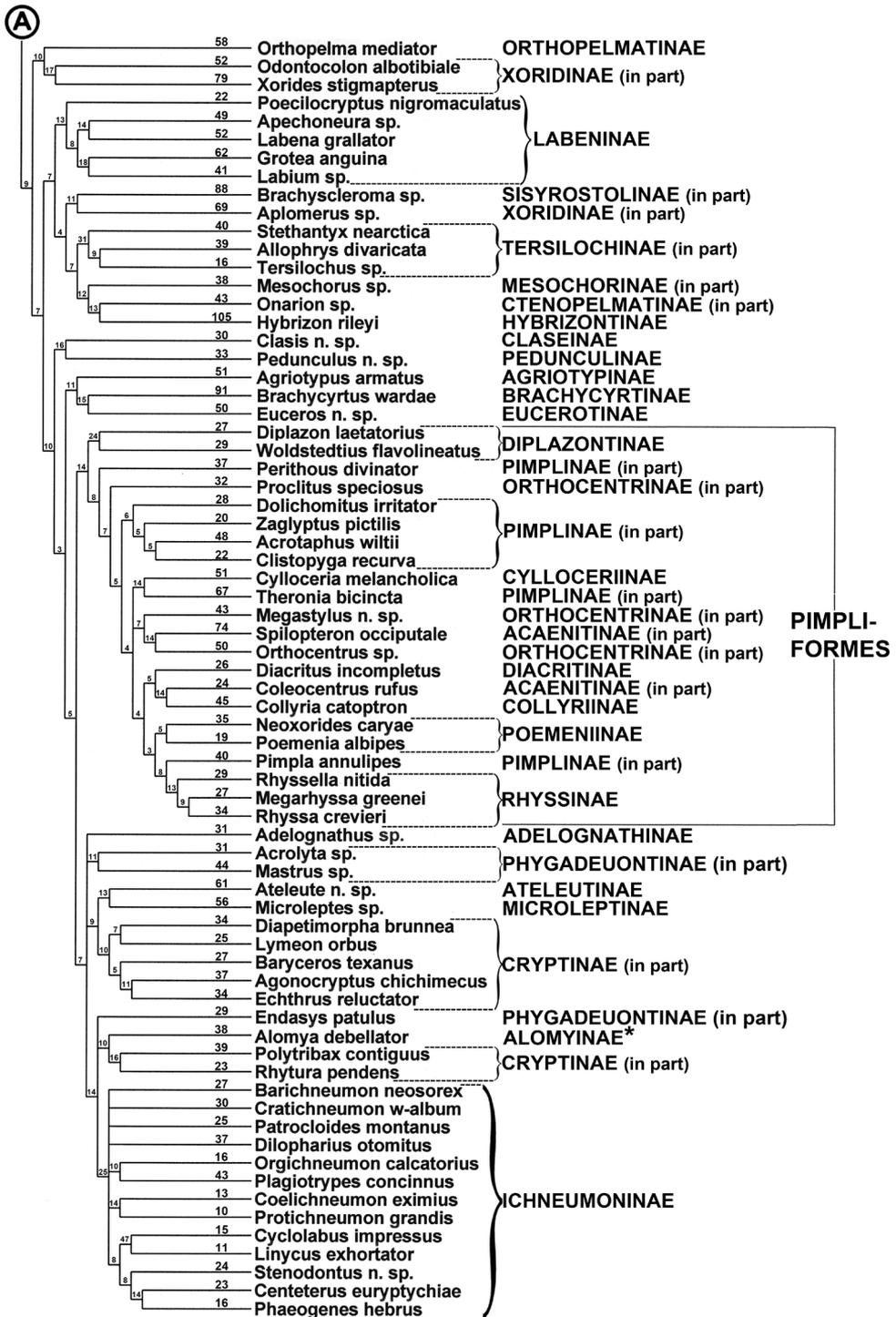


Figure 119. Part 2. Parsimony analysis (molecular characters only). Strict consensus cladogram continued from part 1 of Fig. 119. See Fig. 119, part 1 figure heading for description of figure.

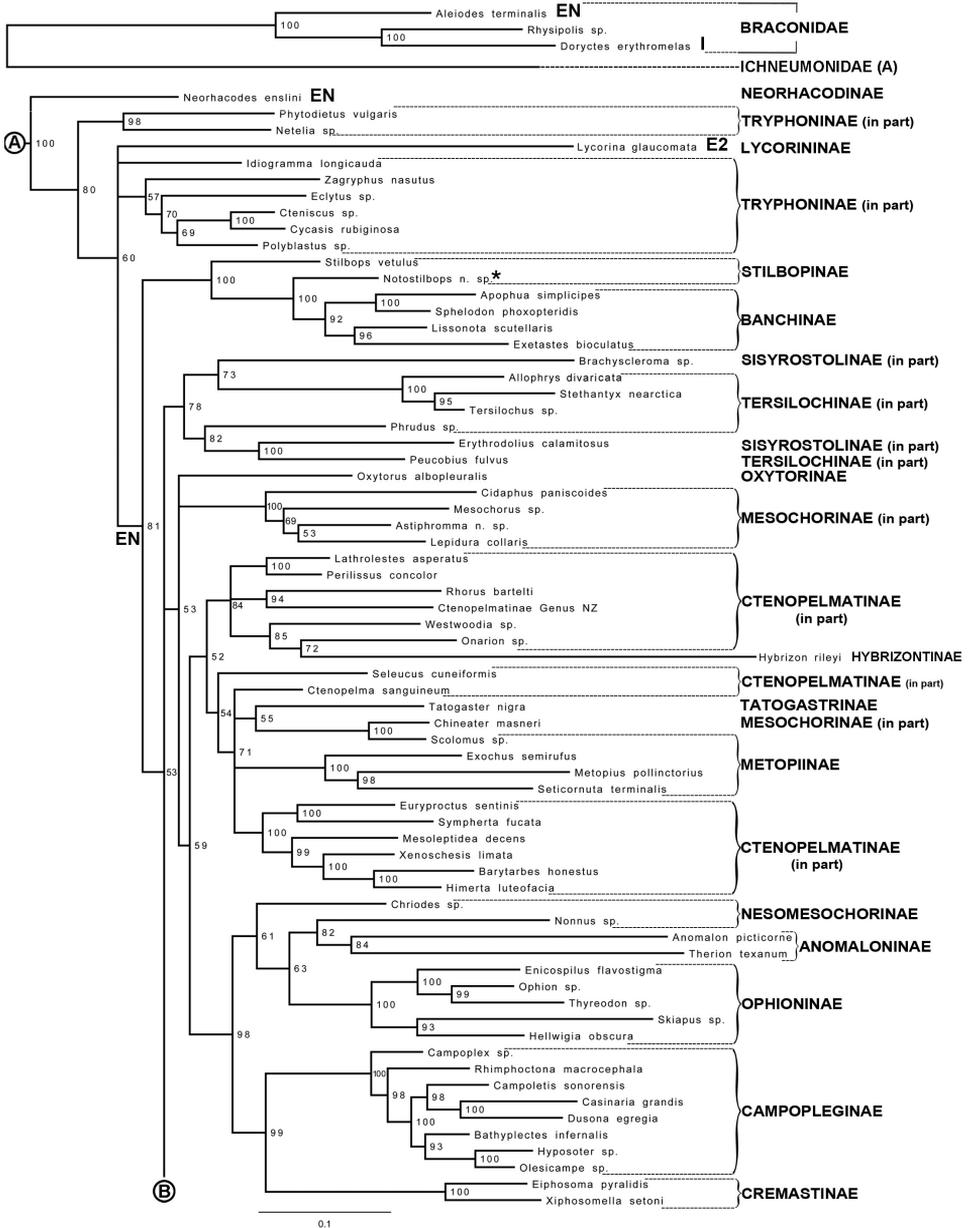


Figure 120. Part 1. Total-evidence Bayesian analysis maximum clade credibility tree. Numbers to the right of nodes are posterior probabilities. “EN” = change from ectoparasitoid to endoparasitoid (character 138); “EC” = change from endoparasitoid to ectoparasitoid; “E2” = change from ectoparasitoid to development inside hind gut with final ectoparasitoid phase; “I” = change from koinobiont to idiobiont (character 137); “K” = change from idiobiont to koinobiont. Taxon names reflect classification prior to study (taxa with asterisks after name are formally re-classified in current study). “B” is continued on part 2 of Fig. 120.

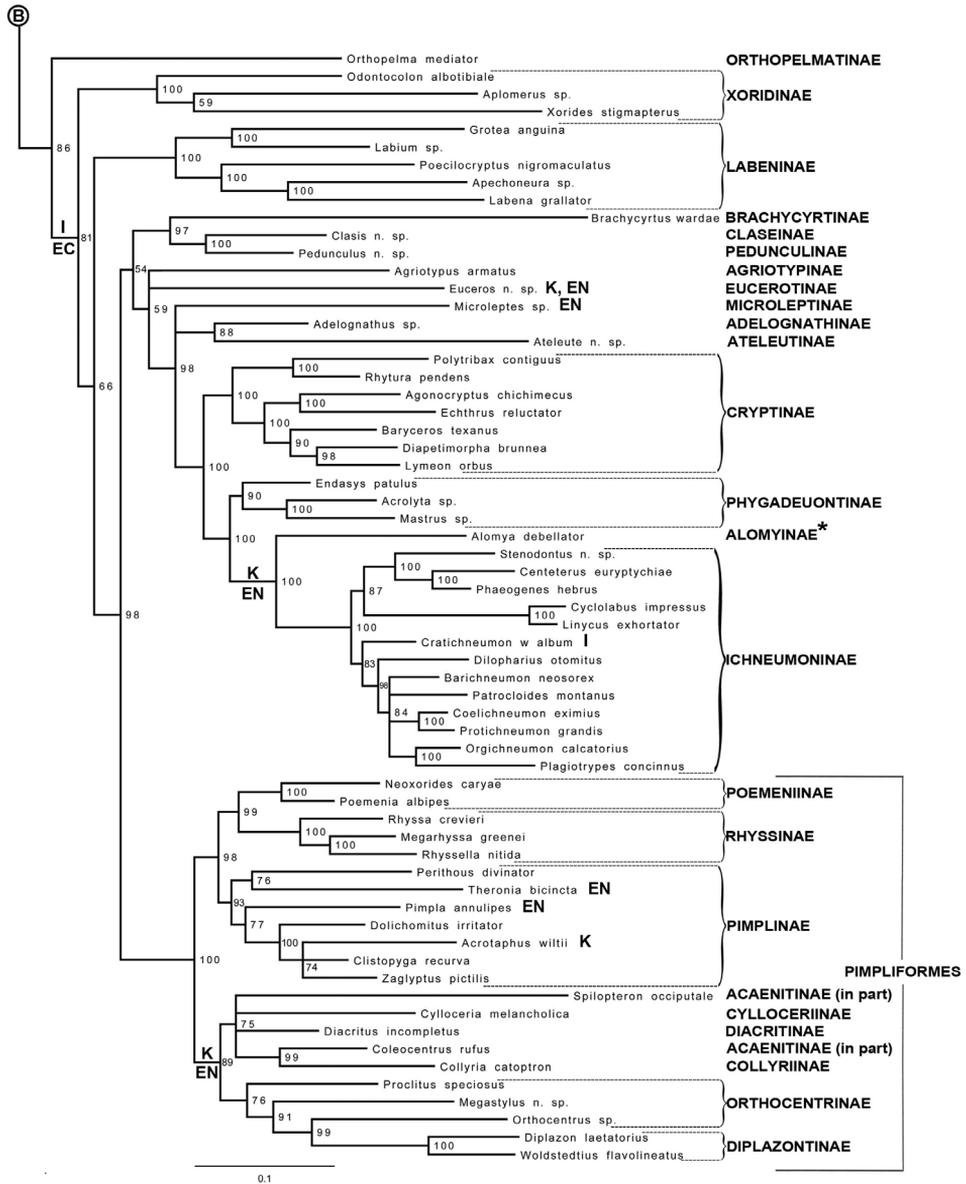


Figure 120. Part 2. Total-evidence Bayesian analysis maximum clade credibility tree continued from part 1 of Fig. 120. Numbers to the right of nodes are posterior probabilities. See Fig. 120, part 1 figure heading for description of figure.

29 synapomorphies, 17 of which were morphological and one of these was uniquely derived: character 118, state 1: larval hypostomal spur meeting stipital sclerite near median end of stipital sclerite (Fig. 102). The Bayesian analysis with only molecular characters was mostly unresolved for Pimpliformes (part 2 of Fig. 121).

In terms of previous hypotheses of internal Pimpliformes relationships, Wahl and Gauld (1998), using morphology-based parsimony recovered (Acaenitinae + (Diacritinae + (Cylloceriinae + (Diplazontinae + Orthocentrinae)))) + (Pimplinae + (Rhyssinae + Poemeniinae)). Quicke et al. (2009) had Diacritinae as sister group to all other taxa which were divided into two sister clades: 1) Acaenitinae + (Cylloceriinae + (Orthocentrinae + (Diplazontinae + Collyriinae))); 2) (Pimplinae + (Rhyssinae + Poemeniinae)). Finally, Klopstein et al. (2019) had equivocal results depending on their analysis. Their transcriptome analysis recovered their diplazontine exemplar, *Syrphophilus tricinctorus* (Thunberg) as sister taxon to the other nine species of Pimpliformes. Some of the topologies found in their anchored enrichment analyses were similar to the transcriptome topology with Diplazontinae as sister to all other taxa, whereas others more resembled the current total-evidence Bayesian analysis and Wahl and Gauld (1998) with two main clades—the higher Pimpliformes and a clade including Acaenitinae and the fly-parasitizing subfamilies. Regardless of the analysis, Klopstein et al. (2019) found very short branch lengths close to the base of Pimpliformes, which they hypothesized suggests a rapid radiation. The ambiguous nature of the current results and those of Klopstein et al. (2019) indicate that resolving ancestral Pimpliformes relationships may be one of the most challenging aspects of future phylogenetic studies within Ichneumonidae.

Ichneumoniformes

Ichneumoniformes sensu stricto (of Wahl 1993a) was not recovered in any analyses (Table 3), although in the total-evidence parsimony analysis (part 3 of Fig. 117), these subfamilies (Brachycyrtinae, Ichneumoninae including Alomyinae, and Cryptinae including Ateleutinae and Phygadeuontinae) were recovered as part of a larger group that included seven other subfamilies (Adelognathinae, Agriotypinae, Claseinae, Eucerotinae, Labeninae, Microleptinae and Pedunculinae). This grouping is hereby called Ichneumoniformes sensu lato. None of the other analyses recovered either Ichneumoniformes s.s. or Ichneumoniformes s.l. In the total-evidence parsimony analysis, Ichneumoniformes s.l. was only supported by 15 synapomorphies, of which 4 were morphological: 56(0) areolet sessile anteriorly (Figs 4, 56); 131(0), larval antenna present and with central papillus (Fig. 7n); 137(0) idiobiont timing of maturation and 138(0) ectophagous location of development (part 1 of Fig. 117). The Bremer support value was only 2 and none of the four morphological characters had a consistency index above 0.16. With respect to specific topologies in our other analyses, in the molecular-only parsimony analysis (part 3 of Fig. 117) and the total-evidence Bayesian analysis (part 2 of Fig. 120), a subset of Ichneumoniformes s.l. was strongly supported that included the following: Microleptinae, Adelognathinae, Ateleutinae, Cryptinae, Phygadeuontinae, Alomyinae and Ichneumoninae (BPP = 98 in the total-evidence Bayesian analysis). We have chosen our definition of Ichneumoniformes s.l. (which includes thirteen subfamilies) based on support for this grouping in the total-evidence parsimony analysis. Future studies may lead us to propose a more restricted definition of Ichneumoniformes s.l. (e.g., the subset listed above). More discussion on the rela-

tionships within Ichneumoniformes is made in the section Support/ relationships of subfamilies (below), especially with respect to Claseinae.

Apart from the study of Quicke et al. (2009), Ichneumoniformes has also been studied previously in a strictly molecular phylogenetic study of Laurenne et al. (2006) and more recently, by a combined morphological and seven gene study by Santos (2017). The latter study focused on the relationships of Cryptini, but included outgroup taxa from other tribes of Cryptinae as well as Pimpliformes, Ophioniformes, Xoridinae and all subfamilies in our Ichneumoniformes s.l. except Alomyinae and Pedunculinae. The combined, maximum likelihood analysis of Santos (2017) found the following topology: Labeninae + (Claseinae + (Eucerotinae + Brachycyrtinae) + (Agriotypinae + ((Cryptini + Aptesini) + (Phygadeuontini including Ichneumoninae, *Hemigaster* Brullé, *Microleptes* Gravenhorst, *Adelognathus* Holmgren and *Ateleute* Förster)))). Accordingly, Santos (2017) raised Phygadeuontini and Ateleutina to subfamily status in order to maintain Ichneumoninae as a subfamily, and restricted Cryptinae to only two tribes. He moved *Hemigaster* to Phygadeuontinae, but did not sink *Microleptes* or *Adelognathus* within Phygadeuontinae. Furthermore, he stated that more study was required to determine the relationships of various phygadeuontine taxa relative to Ichneumoninae. Overall, the relationships within Ichneumoniformes s.l. in our study are quite similar to the results of Santos (2017), especially the finding that *Ateleute* does not cluster within Cryptini, as was classified prior to Santos (2017), and that Ichneumoninae were derived from within Cryptinae s.l., a notion first postulated by Gokhman (1988).

Relationship of Ophioniformes, Pimpliformes and Ichneumoniformes

The total-evidence parsimony analysis was the only one that recovered Pimpliformes, Ophioniformes and Ichneumoniformes s.l. as monophyletic (Table 3, Fig. 117) with Ophioniformes as the sister group to Ichneumoniformes s.l. + Pimpliformes. Both Bayesian analyses (Figs 120, 121) had a grade of Ophioniformes leading to a grouping as follows: Labeninae + (Ichneumoniformes s.l. (except Labeninae) + Pimpliformes). Therefore, apart from the lack of monophyly of Ophioniformes in the Bayesian analyses, the relative relationships of the three major subfamily groupings was similar in both our total-evidence analyses.

The study of Quicke et al. (2009) proposed the following topology: Xoridinae + (Labeninae + (Pimpliformes + ((Claseinae + (Pedunculinae + Brachycyrtinae) + (Ichneumoniformes + Ophioniformes)))). Therefore, Quicke et al. (2009) supported Pimpliformes as sister group to the other two groupings whereas Santos (2017) and Klopstein et al. (2019) generally supported Ophioniformes as sister group to Pimpliformes + Ichneumoniformes albeit with a reduced number of outgroups compared to the current study. The other main difference between the current study and Quicke et al. (2009) was the latter's placement of Labeninae as sister group to all ichneumonids except for Xoridinae. See section on Labeninae (below) for discussion of its equivocal placement in the current study.

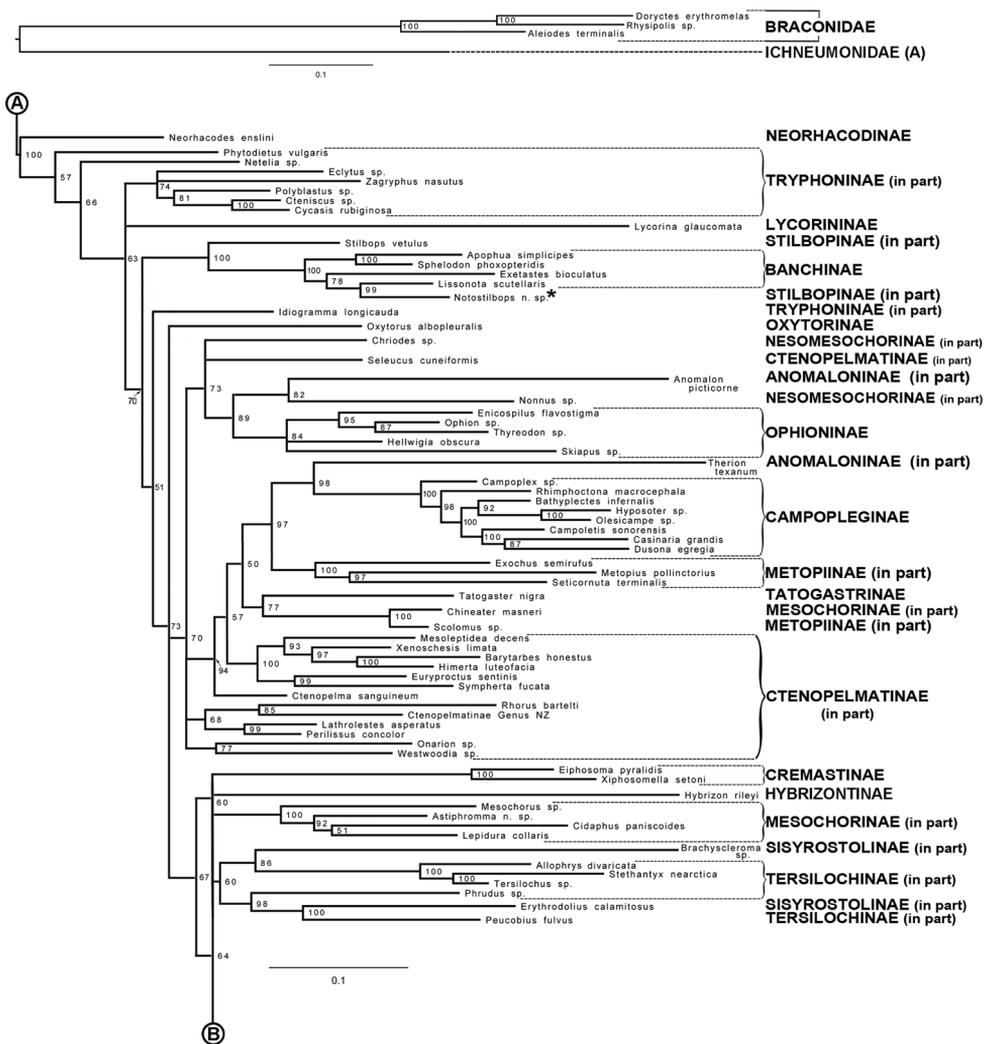


Figure 121. Part 1. Bayesian analysis (molecular characters only) maximum clade credibility tree. Numbers to the right of nodes are posterior probabilities. Taxon names reflect classification prior to study (taxa with asterisks after name are formally re-classified in current study). “B” is continued on part 2 of Fig. 121.

Support/ relationships of subfamilies

Acaenitinae

In the total-evidence analyses (parsimony and Bayesian), the two exemplars of *Acaenitinae* (*Spilopteron occiputale* (Cresson) and *Coleocentrus rufus* Provancher) did not cluster together. *Coleocentrus rufus* was sister to *Collyria catoptron* Wahl (*Collyriinae*), whereas *S. occiputale* had various placements within *Pimpliformes*, such as sister to *Cylloceria melancholica* (Gravenhorst) (*Cylloceriinae*) in the total-evidence parsimony analysis (part 2 of Fig. 117), with two of the orthocentrines in the molecular parsimony

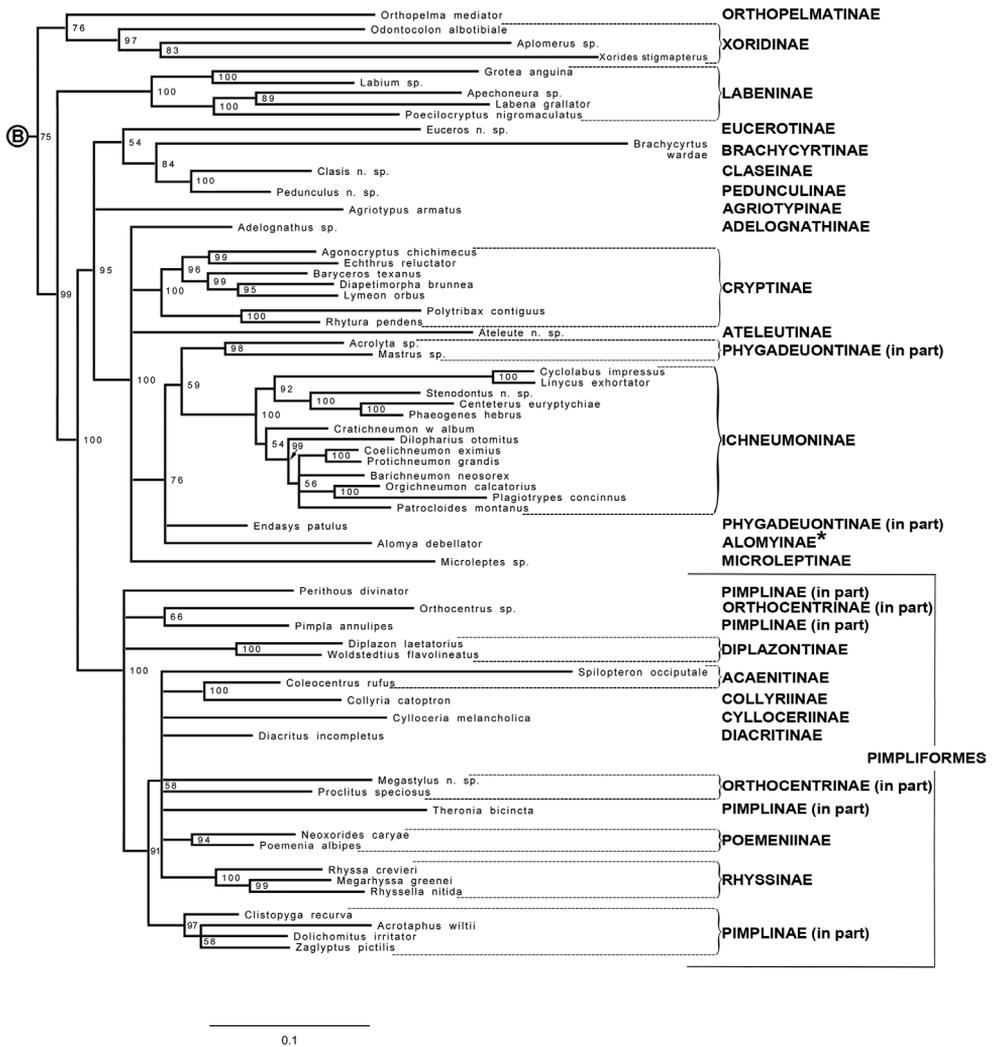


Figure 121. Part 2. Bayesian analysis (molecular characters only) maximum clade credibility tree continued from part 1 of Fig. 121. Numbers to the right of nodes are posterior probabilities. See Fig. 121, part 1 figure heading for description of figure.

momy analysis (part 2 of Fig. 119) and in a grouping with *C. melancholica*, *Diacritus incompletus* Momoi (Diacritinae) and the pair of *Coleocentrus rufus* and *Collyria catoptron* in the total-evidence Bayesian analysis (part 2 of Fig. 120). The only analysis in which the two Acaenitinae exemplars were sister taxa was in the morphological parsimony analysis (part 1 of Fig. 118). This grouping was supported by six morphological synapomorphies of which one was uniquely derived character 94(3) (female hypopygium extending far beyond apex of posterior tergites, strongly triangular in profile) (Fig. 87).

Wahl and Gauld (1998) stated that “the unusual and highly autapomorphic female hypopygium make the Acaenitinae one of the most distinctive of all ichneumonid subfamilies.” Their analysis; however, did not test the monophyly of the subfamily as it was scored as a single line of code in their phylogenetic matrix. Quicke et al. (2009) analyzed the subfamilies as three groups: *Procinetus* Förster, *Coleocentrus* Gravenhorst and “other Acaenitinae”. Their morphology-only analysis and total-evidence analysis recovered Acaenitinae as paraphyletic as follows: Diacritinae + (*Procinetus* + (((*Coleocentrus* + other Acaenitinae) + (Cylloceriinae + ((Diplazontinae + Collyriinae + *Hyperacmus* Holmgren) + Orthocentrinae))). They noted an additional morphological synapomorphy of the subfamily: three venom gland insertions (instead of one or two) (see fig. 9C, D in Quicke et al. 2009), although *Procinetus* was not coded for this character. Finally, Klopstein et al. (2019) included five species of Acaenitinae in their anchored enrichment analysis and found strong support for monophyly of their four Acaenitini exemplars, but *Coleocentrus excitator* (Poda) clustered inconsistently with various groups within Pimpliformes, but almost never shared a unique, common ancestor with Acaenitini. So is Acaenitinae monophyletic?

The current analysis and Klopstein et al. (2019) did not include *Procinetus*, therefore its placement within Acaenitinae cannot be commented on except subjectively to say that the female does have an elongate, triangular hypopygium, although as Townes 1971 observed, this structure has a deep, medial notch resembling the form in atrophine Banchinae. With respect to the other genera of Acaenitinae, the results of Quicke et al. (2009) generally supported their monophyly, whereas the current analysis and Klopstein et al. (2019) generally do not. It must be stated that *Spilopteron* spp. are somewhat aberrant molecularly relative to other Acaenitinae (see Genbank sequences from Quicke et al. (2009); Ito et al. (2015)). For example, the D2 region of 28S of *S. occiputale* is only 74.5% similar to that of *C. rufus* (*C. rufus* is 96.6% similar to our *Perithous divinator* (Rossi) sequence and of comparable similarity to other species of Pimpliformes in our analysis). It is possible that use of a different Acaenitini exemplar instead of *S. occiputale* may have resulted in support of Acaenitinae in the current study, but the study of Klopstein et al. (2019) included *Spilopteron occiputale* and it always clustered with the other three Acaenitini species, therefore monophyly of Acaenitinae appears to be more an issue of whether Coleocentrini and Acaenitini share a common ancestor, rather than monophyly of Acaenitini. More information on the hosts, biology and larvae of Acaenitinae may also help elucidate the monophyly of the family. Known hosts are stem or wood-boring beetles (e.g. Finlayson 1970; Shaw and Wahl 1989), but biology and larval morphology are unknown for most genera and substantiation of existing host records is required.

Adelognathinae

The total-evidence parsimony analysis found Adelognathinae to be the sister group to ((Microleptinae + Ateleutinae) + ((Aptesini + Cryptini including *Echthrus reluctator* (Linnaeus)) + (Phygadeuontinae + (*Alomya debellator* (Fabricius) + Ichneumoninae))) (part 3 of Fig. 117). This grouping was supported by 3 morphological synapomorphies

(15 total) including the uniquely derived character 9(1) (flagellum of male with elliptical or raised, longitudinal, ridge-like tyloids on ventral surface) (Fig. 19). Note that contrary to Townes (1969), some male *Adelognathus* species have tyloids, including our exemplar specimen. The total-evidence Bayesian analysis was also similar, although the relationships of *Adelognathus* sp., *Microleptes* sp. and *Ateleute* sp. nov. at the base of this clade were not unequivocally resolved (part 2 of Fig. 120). The morphology-only parsimony analysis provided no clear placement of *Adelognathus* sp. (it was unresolved near the base of the tree) (Fig. 118).

Townes (1969) implied that Adelognathinae was related to Pimplinae, Tryphoninae, Labeninae and Xoridinae. Presumably, this was because of the medial placement of the spiracle of T1 and the lack of a dorsal, subapical notch on the ovipositor. Both of these character states are plesiomorphic in Ichneumonidae, and therefore of no use in ascertaining phylogeny. Quicke et al. (2009) most usually found the following: Agriotypinae + (Adelognathinae + Cryptinae) and included these three subfamilies in their Ichneumoniformes grouping along with Alomyinae and Ichneumoninae. Most of our analyses placed Adelognathinae within Ichneumoniformes s.l., although its exact placement is equivocal at this point depending on the type of phylogenetic analysis and the characters used. Some of the analyses of Santos (2017) recovered *Adelognathus* among his Phygadeuontinae exemplars but none of our results supported this arrangement.

Agriotypinae

The total-evidence parsimony analysis found that *Agriotypus armatus* was sister species to *Euceros* sp. nov. (Eucerotinae) and these two species were sister group of the clade listed above under Adelognathinae, (i.e., Adelognathinae... to Ichneumoninae) (part 3 of Fig. 117). Agriotypinae + Eucerotinae was supported by 29 character states, of which 8 were morphological, including one that was uniquely derived: oviposition into Trichoptera cases (character 140(6)) with a state change to oviposition on leaves for Eucerotinae (character 140(8)). The Bremer support value was 4 steps. The total-evidence Bayesian analysis was similar in that Agriotypinae and Eucerotinae were placed unresolved as sister group to a clade including Microleptinae, Adelognathinae, Cryptinae and Ichneumoninae, although this clade was very poorly supported (BPP = 59) (part 2 of Fig. 120). In stark contrast to both of the total-evidence analyses, the morphological parsimony analysis recovered Agriotypinae as the sister taxon to all other Ichneumonidae (Fig. 118).

The monotypic Agriotypinae is morphologically aberrant in that it has strongly sclerotized posterior metasomal tergites, which is an autapomorphy within Ichneumonoidea. They are also biologically unusual in that they are aquatic idiobiont ectoparasitoids of prepupae and pupae of Trichoptera in fast-running streams (Bennett 2001). Earlier classifications (e.g., Haliday 1838) placed *Agriotypus* Curtis within its own monotypic family. This family status was maintained by some relatively recent authors (e.g., Mason 1971; Chao 1992); however, Townes (1969) placed the genus within Ichneumonidae, and Sharkey and Wahl (1992) concurred, stating that *Agriotypus* shared the two autapomorphies of Ichneumonidae: the apical displacement of

vein Rs of the fore wing to form the characteristic ichneumonid areolet and the shortening or loss of vein Rs+M in the fore wing (our character 60, states 1 and 2) (Fig. 4). Wahl and Gauld (1998) recovered Agriotypinae in a clade as follows: Labeninae + (Agriotypinae + (Brachycyrtinae + (Cryptinae + Ichneumoninae))). Note that this study used a limited number of subfamilies as outgroups, their purpose being to establish character polarity within Pimpliformes. Bennett (2001) using a morphological cladistic analysis with limited outgroups found Agriotypinae to be sister group to Labeninae. Quicke et al. (2009) found various placements for Agriotypinae depending on the analysis, but concluded that it was likely part of Ichneumoniformes, or perhaps associated with Brachycyrtinae.

With respect to the putative relationship of Agriotypinae and Eucerotinae, of the eight morphological synapomorphies, five of them undergo transformations/ reversals in one taxon or the other. For example, the uniquely derived character 140(6) (oviposition into Trichoptera cases) which supports both taxa, changes to character 140(8) (oviposition on to leaves) in Eucerotinae. Given the extremely different morphology and biology of these two subfamilies, it appears likely that these two highly derived taxa have clustered together because of coincidental homoplasious traits and the lack of any phylogenetic signal linking them to another group. Having said that, both the parsimony and Bayesian total-evidence analyses placed Agriotypinae in relatively the same part of the tree (i.e. somewhere within Ichneumoniformes s.l.), which is similar to the conclusions of Quicke et al. (2009) and Santos (2017).

Alomyinae

In the total-evidence parsimony and Bayesian analyses (Figs 117, 120) and the morphological parsimony analysis (Fig. 118), *Alomya debellator* was sister taxon to Ichneumoninae. Both molecular-only analyses placed *A. debellator* close to Ichneumoninae (along with various cryptine exemplars), but not as its sister taxon (Figs 119, 121).

Since the beginning of the 20th century, *Alomya* has been recognized as closely associated with Ichneumoninae. It has been treated variously as a separate subfamily by Perkins (1959a, 1959b) and Constantineanu (1965), as an ichneumonine tribe consisting solely of *Alomya* (Schmiedeknecht 1902, Morley 1915, Kasparyan 1981), or as part of a tribe including *Phaeogenes* Wesmael and its relatives (Townes et al. 1961, Yu and Horstmann 1997). These decisions were based solely upon adult morphology in a non-phylogenetic framework. Hinz and Short (1983) reared and described the last instar larva commenting that “larval characters generally indicate an affinity with Ichneumoninae, particularly in the disc-shaped maxillary and labial palps each bearing five sensilla of about equal size” (our Character 123, state 2) (Figs 109, 125). They did; however, conclude that bearing in mind the unusual biology (mummification of the host), it should be placed in its own tribe (Alomyini) within Ichneumoninae. Wahl and Mason (1995), in communication with H.K. Townes, stated that *Alomya* was related to *Centeterus* Wesmael and *Colpognathus* Wesmael, genera placed within the ichneumonine tribe Phaeogenini which should therefore take the name Alomyini. More recently, Laurenne et al. (2006) performed a molecular parsimony analysis

including Cryptinae, Ichneumoninae, *Alomya* and a species of the putatively related *Pseudalomya* Telenga and found that *Alomya* was never recovered within Ichneumoninae, whereas *Pseudalomya* clustered with the Phaeogenini exemplars. They therefore formally re-established Alomyinae to encompass *Alomya* as well as the morphologically similar *Megalomya*. They did not include *Pseudalomya* within Alomyinae. The addition of adult morphological characters to these sequences by Quicke et al. (2009) found that *Alomya* was the sister group of Ichneumoninae (and therefore could be postulated to be included within Ichneumoninae. In the same study, *Pseudalomya* still clustered within Phaeogenini. What do our current results indicate about the placement and status of Alomyinae?

Our study, with three genes and a large morphological data set, generally places *Alomya* as the sister group of the Ichneumoninae (both total-evidence analyses and parsimony with only morphological characters). Based on these results, it would be possible to expand Ichneumoninae to encompass *Alomya* (as a tribe), although maintenance of Alomyinae is equally acceptable. We prefer to classify *Alomya* and the closely related genus *Megalomya* Uchida as a tribe within Ichneumoninae, and therefore formally synonymize Alomyinae with Ichneumoninae. Since both classifications are equally acceptable, there is no need for a discussion of similarities and differences between Ichneumoninae and *Alomya* as this would not justify the rank of Alomyini/ Alomyinae one way or the other. A detailed re-description of the larva of *Alomya* is presented in Appendix 1 (Fig. 125).

Anomaloninae

The two Anomaloninae exemplars (*Anomalon picticorne* (Viereck) and *Therion texanum* (Ashmead)) clustered together in the total-evidence and morphology-only parsimony analyses (Figs 117, 118). Thirty-one total characters supported Anomaloninae in the total-evidence parsimony analysis, including nine morphological, of which one was uniquely derived: character 134(2) (egg with a wide, pedunculate, ventral protrusion and an apical, sinuous stalk) (Fig. 114). The Bremer support was 4 steps. It should be noted that not all anomalonines have this egg structure and the egg of *A. picticorne* was scored as unknown. In terms of diagnostic characters for Anomaloninae, character 47(1) (propodeum with reticulate sculpture) (Fig. 42) was a synapomorphy for the subfamily, but this character state also evolved independently in *Thyreodon* sp. (Ophioninae) and *Casinaria grandis* Walley (Campopleginae), therefore it must be used in concert with other characters to distinguish Anomaloninae.

Anomaloninae was the sister group of Ophioninae in the total-evidence parsimony analysis, supported by 33 characters (13 morphological) including the uniquely derived character 54(2): cell $1+2R_s$ (areolet) of fore wing with vein R_s absent so that the only cross-vein is distad vein $2m-cu$ (Fig. 53) (with a reversal in *Therion texanum*). The Bremer support was only 3. The Bayesian total-evidence analysis also recovered Anomaloninae, but only with a posterior probability of 84 (Fig. 120) and as sister group to *Nonnus* sp. (Nesomesochorinae) (posterior probability of 82). Anomaloninae was not supported in either of the molecular-only analyses (Figs 119, 121).

Previous morphological analyses (e.g., Gauld 1976) supported the monophyly of Anomaloninae. Quicke et al. (2009) coded morphology at the tribal level for Anomaloninae and found that Anomalonini was the sister group to Gravenhorstiini in both their morphological and total-evidence parsimony analyses. Whereas it is possible that Anomalonini (i.e., *Anomalon picticorne*) and Gravenhorstiini (as represented by *The- rion texanum*) are not sister taxa, the weight of evidence supports this relationship. Lack of congruence between our molecular and total-evidence analyses may be because of our choice of exemplars or genes which should be examined by addition of more Gravenhorstiini species and additional gene regions in future studies.

Ateleutinae

Ateleute sp. nov. was placed within Ichneumoniformes s.l. in all of our analyses, except parsimony with only morphological characters in which it was sister species to *Nonnus* sp. in a portion of the tree that lacked resolution (part 1 of Fig. 118). *Ateleute* was sister species to *Microleptes* sp. (Microleptinae) in the other two parsimony analyses (part 3 of Fig. 117, part 2 of Fig. 119), sister species to *Adelognathus* sp. (Adelognathinae) in the total-evidence Bayesian analysis (part 2 of Fig. 120) or in a clade that lacked internal resolution with *Adelognathus* sp., *Microleptes* sp., *Alomya debellator*, Cryptinae, Ichneumoninae and exemplars of Phygadeuontinae (Bayesian molecular-only analysis: part 2 of Fig. 121). In summary, in all analyses except for parsimony with only morphological characters, it grouped with exemplars of the six subfamilies listed above, but at no time did it group within Cryptinae or any other subfamily.

Previously, Townes et al. (1961) placed *Ateleute* within Phygadeuontini, but later moved it to Cryptini (Townes 1970a) within its own subtribe (Ateleutina). The molecular analysis of Laurenne et al. (2006) also found equivocal placement for *Ateleute*. Depending on alignment parameters, it was sometimes placed as sister to: ((most of Hemigastrini) + Cryptini), or in an unresolved clade of *Ateleute*/ Phygadeuontini/ (Hemigastrini + Cryptini), or even as sister to Ichneumoninae. The combined morphology and molecular analysis of Quicke et al. (2009) coded morphological characters for *Ateleute* separately from all other Cryptinae species and recovered *Ateleute* in a clade of five species that was sister to a clade including all Hemigastrini and Cryptini exemplars. In the latter analysis, *Ateleute* spp. clustered with exemplars of a second genus of Ateleutinae (*Tamaulipeca* Kasparyan) as well as *Handaoia* Seyrig and *Austriteles* Gauld (both Phygadeuontini). More recently, Santos (2017) recovered a clade of six exemplars of *Ateleute* and *Tamaulipeca* as sister group to Adelognathinae in his parsimony analysis and nested with some of his Phygadeuontini exemplars in his maximum likelihood analysis. On the basis of our parsimony and Bayesian analyses, we concur with the raising of Ateleutina to subfamily status by Santos (2017), but its exact placement within Ichneumoniformes s.l. is still equivocal.

Banchinae

The four exemplar species of Banchinae were closely related in all analyses. The two Glyptini species (*Apophua simplicipes* (Cresson) and *Sphelodon phoxopteridis* (Weed))

were always sister species and Atrophini (*Lissonota scutellaris* (Cresson)) was generally sister to Banchini (*Exetastes bioculatus* Cresson). In the total-evidence parsimony analysis, Glyptini, (Atrophini + Banchini) and *Notostilbops* sp. (Stilbopinae) were found in a clade that lacked internal resolution (part 6 of Fig. 117). This grouping was strongly supported: 47 total characters (7 morphological) of which 2 were uniquely derived-character 95(1) (hind margin of hypopygium with median apical notch) (Fig. 88); character 114(1) (larval posterior struts of inferior mandibular processes greater than two times length of anterior struts and connected by a band) (Fig. 103). The Bremer support was 10+ for this node. Moving *Notostilbops* sp. so that it was sister species to *Stilbops vetulus* resulted in a tree that was 13 steps longer (9930). Note that *Notostilbops* sp. was scored as 0 for character 95 (apical notch of hypopygium absent) and as unknown for character 114 (larva of *Notostilbops* Townes is not known). *Stilbops vetulus* (Gravenhorst) (Stilbopinae) was sister to the clade comprised of *Notostilbops*/ Atrophini + Banchini/ Glyptini. The total-evidence Bayesian analysis had *Notostilbops* sp. as the sister of the four banchine species (posterior probability of 100), but Banchinae was only supported with a posterior probability of 92 (part 1 of Fig. 120). Both analyses with only molecular characters found *Notostilbops* to be sister to *Lissonota*, clustering within Banchinae (Figs 119, 121). The morphological parsimony analysis was the only one that found unequivocal support for the monophyly of Banchinae (without *Notostilbops*) (Fig. 118). The strict consensus tree for this analysis had equivocal placement of *Notostilbops*, but in 98 % of the 3872 equally parsimonious trees, it was sister to *Stilbops vetulus* and in 88% of the trees, these two taxa formed a sister group to the eight Tryphoninae species (and no trees had either of the stilbopines sister group to Banchinae). To summarize our results, the parsimony analysis with only morphological characters supported Banchinae with no evidence that either stilbopine exemplar was related to Banchinae (Fig. 118); molecular evidence found that *Notostilbops* is a banchine (and *Stilbops* is sister to Banchinae) (Figs 119, 121) and this was the same result as the total-evidence analyses, except that the relationships in the *Notostilbops* + Banchinae clade was equivocally resolved (Figs 117, 120).

Wahl (1988) commented on the placement of *Notostilbops*. He stated that most *Notostilbops* females have a membranous region apically in the hypopygium where the notch is present in Banchinae, although some *N. fulvipes* (Townes) have a distinct notch. In terms of the ovipositor, all *Notostilbops* females have a distinct dorsal subapical notch which is present in Banchinae, but absent in the two other genera currently assigned to Stilbopinae: *Stilbops* and *Panteles* Förster. On the basis of these two apomorphic character states and the weight of evidence in our study, *Notostilbops* appears better placed in Banchinae (either within Atrophini or *incertae sedis*). We formally transfer *Notostilbops* Townes to tribe Atrophini of Banchinae. Its tribal placement is based on the fact that it does not possess synapomorphies that would place it within Glyptini (e.g., T2–T4 of metasoma with chevron-shaped grooves) or Banchini (e.g., character 63, state 1: hind wing vein 2/Cu much closer to vein M than A). The monophyly of Atrophini relative to Banchini and Glyptini has not been thoroughly tested with a morphological, cladistic analysis and this would be required to confirm monophyly of

Atrophini, and placement of *Notostilbops* within it. Wahl (1988) stated that knowledge of the larva of *Notostilbops* would help determine its placement (presence of the band connecting the larval mandibular processes would support its placement in Banchinae). Quicke et al. (2009) generally recovered Banchinae as monophyletic near the base of Ophioniformes, but not in a sister-group relationship with Stilbopinae (which clustered with Tryphoninae). They did not include *Notostilbops* in their analyses.

Brachycyrtinae

The placement of *Brachycyrtus wardae* Bennett varied somewhat between our analyses. Total-evidence parsimony placed it as the sister to Labeninae, supported by 32 characters (6 homoplasious morphological) with a Bremer support of 10 (part 3 of Fig. 117). This pairing was sister to (Claseinae + Pedunculinae) and together these taxa were sister to the rest of Ichneumoniformes s.l. The total-evidence Bayesian analysis recovered (Brachycyrtinae + (Claseinae + Pedunculinae)) with a posterior probability of 97 (part 2 of Fig. 120). The exact relationships of this grouping to Agriotypinae, Eucerotinae and the rest of Ichneumoniformes s.l. is unclear because of very low posterior probabilities (54 to 59) for the nodes in this part of the tree. Brachycyrtinae was not related to Labeninae in the total-evidence Bayesian analysis, with Labeninae placed as sister group to a well-supported clade (posterior probability of 98) comprised of Pimpliformes + Ichneumoniformes s.l..

As noted in the Introduction, Wahl (1993a) placed Brachycyrtinae within his Ichneumoniformes s.s. as the sister group to (Cryptinae + Ichneumoninae). Our results do not support this precise relationship; however, our total-evidence parsimony analysis (part 3 of Fig. 117) suggests that Brachycyrtinae belongs within Ichneumoniformes s.l. Quicke et al. (2009) found that Claseinae and Pedunculinae usually clustered with Brachycyrtinae and sometimes also with Eucerotinae and Microleptinae. Their Brachycyrtiformes: (Claseinae + (Pedunculinae + Brachycyrtinae)), was not supported in our total-evidence parsimony analysis without Labeninae nested within as sister to Brachycyrtinae (Bremer support of 10 steps). The total-evidence Bayesian analysis did support it, but not unequivocally (BPP = 97). Since both our total-evidence parsimony and Bayesian analyses did not support the group unequivocally, we prefer not to recognize Brachycyrtiformes exactly as Quicke et al. (2009) proposed it until the relationship of Labeninae to these taxa can be more clearly defined. See the sections below for Claseinae, Labeninae and Pedunculinae for more discussion on the relationships of these taxa.

Campopleginae

Both total-evidence analyses strongly supported the monophyly of the eight exemplar species of Campopleginae. In the parsimony analysis, the subfamily was supported by 43 synapomorphies (5 morphological, none of which were uniquely derived) with a Bremer support value of 10+ (part 6 of Fig. 117). The Bayesian analysis also supported the subfamily with a posterior probability of 100 (part 1 of Fig. 120). Both molecular-only analyses supported the monophyly of Campopleginae (Figs 119, 121), whereas the morphological parsimony analysis found that *Casinaria grandis* and *Dusona egregia*

(Viereck) did not cluster with the other six species (Fig. 118). Cremastinae was the sister group to Campopleginae in both total-evidence analyses although the support in the parsimony analysis was relatively low (26 characters including 3 morphological of which none were uniquely derived and a Bremer support value of 1). Internally, both total-evidence analyses found the same topology, with *Campoplex* sp. sister to the other seven species and *Rhimphoctona macrocephala* (Provancher) sister to the rest.

Townes (1970b) divided Campopleginae into four tribes. Wahl (1991) commented on these tribes from a cladistic viewpoint and recommended suspension of Townes's tribal classification, instead recognizing five informal genus groups. He also hypothesized that Cremastinae was the sister group to Campopleginae. Miah and Bhuiya (2001) performed a morphological cladistic analysis finding that Townes's tribes Hellwigiini and Nonnini (= Nesomesochorini) did not belong in Campopleginae. Later, Quicke et al. (2005) based on morphology and molecular data transferred Hellwigiini (*Skiapus* and *Hellwigia* Gravenhorst) to Ophioninae and resurrected Nonninae for *Nonnus* Cresson and Nesomesochorinae for *Chriodes* Förster and *Klutiana* Betrem. Quicke et al. (2009) placed the latter two genera together within Nesomesochorinae. The latter study found that either Cremastinae or Nesomesochorinae was sister to Campopleginae, depending on how gaps were treated in the molecular data. In contrast, the anchored enrichment study of Klopstein et al. (2019) recovered Cremastinae + (Ophioninae + Campopleginae).

The current results strongly support the monophyly of Campopleginae (i.e., the group comprised of the genera that were previously classified in Townes's Campoplegini and Porizontini). They also support the removal of Hellwigiini and Nesomesochorini from Campopleginae. In terms of the sister-group relationship, both total-evidence analyses support Cremastinae as sister to Campopleginae with Nesomesochorinae and (Ophioninae + Anomaloninae) also related, albeit more distantly. With respect to internal relationships, Townes's Campoplegini and Porizontini were not supported (*Campoplex* sp. was sister to all other genera, but the other Campoplegini exemplar, *Casinaria grandis*, clustered within the six Porizontini species. Likewise, there was no support for the genus groups of Wahl (1991). For example, the two exemplar species from Wahl's *Bathyplectes* genus group (*Bathyplectes infernalis* (Gravenhorst) and *Rhimphoctona macrocephala*) were not sister taxa. A more comprehensive analysis is required to define natural groups within the subfamily.

Claseinae

Claseinae (*Clasis* sp. nov.) was sister group to Pedunculinae (*Pedunculus* sp. nov.) in all analyses except the morphology-only parsimony analysis in which it was unresolved near the base of Ichneumonidae (part 1 of Fig. 118). In the total-evidence parsimony analysis, (Claseinae + Pedunculinae) was supported by 17 synapomorphies, 4 of which were morphological (none uniquely derived) and a Bremer support of 9 (part 3 of Fig. 117). The Bayesian total-evidence analysis supported this relationship with a posterior probability of 100 (part 2 of Fig. 120). See Brachycyrtinae (above) for more discussion of the relationships of these two subfamilies to other taxa.

Clasis Townes was originally placed within the cryptine tribe Phygadeuontini (Townes and Townes 1966) and then later, Townes (1969) moved it to Labeninae as a tribe (Clasini) along with the newly described monotypic *Ecphysis* Townes. Gauld (1983) moved Clasini back into Cryptinae as its own tribe. Porter (1998) raised the group to subfamily status. Quicke et al. (2009) found that Claseinae was the sister group of (Pedunculinae + Brachycyrtinae) in most of their analyses. Santos (2017) never recovered his three *Clasis* species within Phygadeuontini or Cryptinae but instead, they clustered together as sister to Agriotypinae, (Agriotypinae + Labeninae) or (Brachycyrtinae + Eucerotinae), depending on the method of analysis.

The fact that our total-evidence parsimony analysis supports the monophyly of Labeninae as it was defined by Townes (1969) (i.e., including *Clasis*, *Pedunculus* Townes and *Brachycyrtus* Kriechbaumer) is intriguing, considering how much work has been done studying and ultimately dividing this group. Certainly, the arrangement of Townes (1969) is not exactly the same as our parsimony results (e.g., Townes placed *Pedunculus*, *Brachycyrtus* and *Poecilocryptus* Cameron into a single tribe), but the fact that all eight of the species we chose from the Labeninae of Townes (1969) clustered together in our total-evidence parsimony analysis raises the question, should Labeninae be re-established to include Brachycyrtinae, Claseinae, Pedunculinae and Labeninae as it is currently defined? One of the arguments against this change is that our total-evidence Bayesian analysis recovered Labeninae (in the current sense) unrelated to (Brachycyrtinae + (Claseinae + Pedunculinae)) (as sister to Pimpliformes + Ichneumoniformes s.l. except for Labeninae). In addition, Townes (1969) did not provide any characters that define his concept of Labeninae. Since the relationships of Labeninae, Brachycyrtinae and (Claseinae + Pedunculinae) are equivocal among our five analyses, and the results of Santos (2017) were similarly equivocal, it seems prudent to maintain the subfamily status of all four of these subfamilies, rather than sink them back into Labeninae. Nevertheless, it is interesting that this study has recovered one of Townes's previously recognized groupings, similar to the study of Klopstein et al. (2019) that moved *Pseudorhyssa* Merrill back into Pimplinae and resurrected tribe Theroniini.

Collyriinae

Both total-evidence analyses (Figs 117, 120) and both molecular-only analyses (Figs 119, 121) found that *Collyria catoptron* was sister species to *Coleocentrus rufus* (Acaenitinae) within Pimpliformes. *Coleocentrus rufus* was not however, closely related to the other acaenitine exemplar: *Spilopteron occiputale* (see Acaenitinae, above). The total-evidence parsimony analysis supported (*Collyria catoptron* + *Coleocentrus rufus*) based on 23 synapomorphies (6 morphological of which none were uniquely derived) with a Bremer support of only 1. The relative placement of this sister-group pairing within Pimpliformes is not clear because of major differences in the overall topology of the group depending on the phylogenetic method used (see Pimpliformes section, above). The placement of Collyriinae in the morphological parsimony analysis was also not clearly resolved (Fig. 118).

Historically, the taxonomic placement of *Collyria* has been contentious. Dalla Torre (1902) and Morley (1908) related it to *Acaenitus* Latreille and *Arotus* Gravenhorst (Acaenitinae), but the latter noted that previous British catalogues placed it within Ophioninae (i.e. Ophioniformes) related to *Pristomerus vulnerator* (Panzer) (Cremastinae). Cushman (1924) placed it in a new tribe, Collyriini within Pimplinae (i.e., Pimpliformes). Townes (1971) stated: “Neither the adult nor the larva, however, have any real resemblance to the acaenitines” and he placed *Collyria* in a separate subfamily, arranged close to *Orthopelma* Taschenberg (Orthopelmatinae) and Orthocentrinae (although this part of his Genera of Ichneumonidae seems to be where he placed taxa of uncertain affinity). Short (1978) simply stated it was “isolated on both larval and adult characters”. Wahl and Gauld (1998) did not include it in their analysis of the Pimpliformes; however, Belshaw et al. (1998) and Quicke et al. (2009) recovered Collyriinae within Pimpliformes, the latter study placing it within the Diptera-parasitizing clade (Diplazontinae, Orthocentrinae and Cylloceriinae). Note that species of *Collyria* are egg-larval, koinobiont endoparasitoids of Cephidae (Hymenoptera) (Salt 1931; Wahl et al. 2007), whereas the few known records of Acaenitinae show that they are larval koinobiont endoparasitoids of Coleoptera (Shaw and Wahl 1989).

More recently, Kuslitzky and Kasparyan (2011) described a second genus of Collyriinae: *Aubertiella* Kuslitzky & Kasparyan, from the Middle East and Sheng et al. (2012) described a third genus (*Bicurta* Sheng, Broad & Sun) from southeastern China. The latter study also re-examined the phylogenetic analysis of Wahl and Gauld (1998) with the addition of *Collyria* and *Bicurta* and found that they clustered together within Pimpliformes, but in terms of their placement, relationships in their unweighted parsimony analysis were largely unresolved. Searching with implied weights (Goloboff 1993) with values ranging from $k = 1$ to $k = 10$ resulted in a single topology in which *Bicurta* + *Collyria* was the sister group to Rhysinae. Sheng et al. (2012) did, however, note that Wahl and Gauld (1998) coded all Acaenitinae at the subfamily level in their matrix and suggested that re-coding all genera of Acaenitinae separately could reveal different patterns of relationships within Pimpliformes, especially relative to Collyriinae. They also noted some similar general characteristics between Collyriinae and some Acaenitinae and Poemeniinae namely, short antennae, median tubercle on the clypeus (our character 3, state 1), lack of transverse carinae of the propodeum (our characters 36 and 38, state 3) and hind wing vein $2/Cu$ originating close to vein M (our character 63, state 1). Characters 3, 36 and 63 supported the grouping of *Coleocentrus* + *Collyria* in our total-evidence parsimony analysis (part 2 of Fig. 117). Most recently, the transcriptome analysis of Klopstein et al. (2019) found a sister-group relationship of *Collyria trichophthalma* (Thomson) and *Coleocentrus excitator* (Poda), the only exemplars of these two subfamilies in this analysis. Their anchored enrichment analyses found the placement of *Collyria* to be unstable with some analyses placing it as sister to all other Pimpliformes and in others it was related to *Coleocentrus* or Acaenitini. In summary, the relationships of Collyriinae are still equivocal, but it may be related to Acaenitinae. Finally, it is noted that the description of the final larval instar cephalic

sclerites of *Collyria coxator* (Villers) by Short (1959) is inaccurate. We have examined the slide mount used by Short. The mandibles are completely absent, and there is no trace of the antenna. A whole larva of *Collyria catoptron* has been photographed (Fig. 112) and a revised description of the cephalic sclerites of the mature larva of *Collyria* is provided in Appendix 1.

Cremastinae

The two species of Cremastinae, *Eiphosoma pyralidis* Ashmead and *Xiphosomella setoni* Johnson, clustered together in all analyses with very strong support. The total-evidence parsimony analysis supported this grouping with 61 synapomorphies (5 morphological) and a Bremer support value of 10+ (part 6 of Fig. 117). Character 71, state 1 (apex of middle and hind tibiae with sclerotized bridge separating insertion areas) (Fig. 65) was uniquely derived. Cremastinae was sister group to Campopleginae in both total-evidence analyses (Figs 117, 120) and these two subfamilies grouped with Nesomesochorinae and (Anomaloninae + Ophioninae) in the higher Ophioniformes.

The monophyly of Cremastinae has generally gone unquestioned, supported largely by the unique synapomorphy (within Ichneumonidae) of the sclerotized bridge of the middle and hind tibiae separating the insertion points of the tarsus and tibial spurs (Gauld et al. 2000). Quicke et al. (2009) coded morphology separately for the *Belesica* group (*Belesica* Waterston and *Eurygenys* Townes) relative to “other Cremastinae”. They stated that Cremastinae was monophyletic in all individually aligned analyses, but when they combined these data into a single data set (the elision strategy of Wheeler et al. 1995), *Eurygenys* sp. did not cluster with the other Cremastinae, but was sister to a clade comprised of *Skiapus*, Hybrizontinae, Anomaloninae, Ophioninae, Cremastinae, Nesomesochorinae and Campopleginae. We were not able to include a representative of the *Belesica* group in our analysis, therefore the relationships of this group to other genera of Cremastinae remains ambiguous. See Campopleginae (above) for discussion of prior hypotheses of relationships of Cremastinae, Campopleginae and Nesomesochorinae.

Cryptinae sensu stricto and Cryptinae sensu lato

The seven species of Cryptinae sensu stricto, i.e., members of the tribes Cryptini and Aptesini (formerly Hemigastrini), grouped together in both of the total-evidence analyses and the Bayesian (molecular-only) analysis (Table 3). The total-evidence parsimony analysis had moderately low support for Cryptinae with 17 synapomorphies (5 morphological, including one uniquely derived: sternaulus posteriorly ending anterior to posterolateral corner of mesopleuron (character 27(2)) (Fig. 28). The Bremer support value was 3 (part 3 of Fig. 117). There was much stronger support for Cryptinae in the total-evidence Bayesian analysis (BPP = 100) (part 2 of Fig. 120).

In the analyses in which Cryptinae s.s. was monophyletic, it was always related to species in the subfamilies Ateleutinae, Microleptinae, Phygadeuontinae, Alomyinae, Ichneumoninae and Adelognathinae. The specific relationships of each of these subfamilies are discussed more fully in the section above on Ichneumoniformes, as well as in the respective subfamily sections.

The 11 species of Cryptinae sensu lato (species of Ateleutinae, Phygadeuontinae and Cryptinae s.s.) never shared a unique, common ancestor, regardless of the analysis. This was caused by: 1) placement of *Ateleute* sp. nov. (Ateleutinae) away from the other species; 2) paraphyly of the other 10 species of Cryptinae s.l. with respect to Alomyinae + Ichneumoninae. In summary, we found no evidence to support the monophyly of Cryptinae s.l. (= Gelinae) of Townes (1970a).

Regarding Phygadeuontinae, in the total-evidence parsimony analysis, the three species (*Endasys patulus* (Viereck) + (*Acrolyta* sp. + *Mastrus* sp.)) grouped together with weak support (13 synapomorphies and a Bremer support value of 1) (part 3 of Fig. 117). This group was also supported in the Bayesian total-evidence analysis, but not unequivocally (BPP = 90) (part 2 of Fig. 120). Both of these analyses placed Phygadeuontinae as the sister group to (Alomyinae + Ichneumoninae) (18 synapomorphies and a Bremer support value of 2 for the parsimony analysis and p.p. of 100 for the Bayesian analysis). Therefore, in terms of the monophyly and placement of Phygadeuontinae (Phygadeuontini prior to Santos 2017), our analysis provided some support for its monophyly; however, we included only three species and the more rigorous study of Santos (2017) has shown that this group is most likely not monophyletic. Its raising to subfamily status by the latter study was necessitated by its paraphyly with Ichneumoninae, but it may be a “dumping ground” for all the “non-Aptesini” and “non-Cryptini” taxa that were previously placed within Cryptinae. See the section on Phygadeuontinae (below) for more discussion of this taxon.

With respect to the relationship between Cryptinae s.s. and Ichneumoninae, Townes (1969) stated that they were not related on the basis of differences in larval morphology. Gauld (1991) disagreed, placing the two families together in his “Phygadeuontoid” subfamilies. Wahl (1993a), in his discussion on the relationships of his Ichneumoniformes commented on the opinion of Townes (1969) stating: “The larvae are indeed very dissimilar but this is because, at the subfamilia level, Phygadeuontinae [= Cryptinae s.l.] larvae are plesiomorphic in almost every respect while larvae of Ichneumoninae are extremely specialized endoparasitoids. Larvae of Ichneumoninae can be easily derived from a Phygadeuontinae-like precursor.” Nevertheless, Wahl (1993a) did not explicitly suggest paraphyly of Cryptinae and Ichneumoninae. The first author to suggest this was Gokhman (1988) who argued that the ichneumonine tribe Phaeogenini provided evidence for an “evolutionary pathway” between Ichneumoninae and Phygadeuontini.

In terms of more recent, sequence-based studies, some of the analyses of Laurenne et al. (2006) (with high gap costs) found Ichneumoninae nested within most of Phygadeuontini. The combined analysis of Quicke et al. (2009) had similar results, although their two presented cladograms propose Ichneumoninae as sister group to (Agriotypinae + Adelognathinae + Cryptinae s.l.).

Finally, in terms of support for the tribes of Cryptinae s.s., the total-evidence parsimony analysis had strong support for Cryptini (including *Echthrus reluctator*) with 30 synapomorphies and a Bremer support of 6, and Aptesini had 25 synapomorphies and a Bremer support of 9. The Bayesian total-evidence analysis also supported both tribes (BPP = 100 for each) (part 2 of Fig. 120).

Ctenopelmatinae

Ctenopelmatinae was never recovered as monophyletic (Table 3). The 14 species of Ctenopelmatinae did share a relatively recent common ancestor in the total-evidence parsimony analysis (part 5 of Fig. 117) along with the following small subfamilies and enigmatic genera nested in the same clade: *Hybrizon rileyi* (Ashmead) (Hybrizontinae); *Lycorina glaucomata* (Lycorininae); *Oxytorus albopleuralis* (Provancher) (Oxytorinae); *Tatogaster nigra* Townes (Tatogastrinae); *Chineater masneri* (Mesochorinae) and *Scolomus* sp. (Metopiinae). This grouping was relatively weakly supported by 18 synapomorphies (4 morphological of which none were uniquely derived) and a Bremer support of 2. In the strict consensus cladogram it was placed within Ophioniformes in a clade with equivocal relationships as follows: (Mesochorinae except *Chineater*) / (Ctenopelmatinae and related taxa) / ((Metopiinae + (*Stilbops* + Banchinae including *Notostilbops*) + higher Ophioniformes). Of interest, the clade was supported by only 12 synapomorphies including the presence of a tooth on the fore tibia (character 68(1)) (Fig. 63) with a reversal back to the lack of a tooth in Metopiinae to Campopleginae. In other words, the one morphological character that has been used to define Ctenopelmatinae in the past did not define Ctenopelmatinae (by itself) in our analysis. Sixty-seven percent of the most parsimonious trees supported a sister-group relationship of (Mesochorinae except *Chineater* + Ctenopelmatinae and related taxa). In comparison to the parsimony analysis, the total-evidence Bayesian analysis recovered a grouping that included all 14 Ctenopelmatinae species as well as *Hybrizon* and *Tatogaster* and all four species of Metopiinae, but this group did not include *Oxytorus* or *Lycorina* (part 1 of Fig. 120). The support for this clade, however, was very low (BPP = 52). None of the other analyses recovered Ctenopelmatinae as monophyletic, with or without Metopiinae, Mesochorinae or the exemplars of the small subfamilies.

In terms of support for the ctenopelmatine tribes, of the five for which multiple species were included, only two (Perilissini and Mesoleiini) had their species clustering together in the total-evidence parsimony analysis. The other three large tribes (Pionini, Euryproctini and Ctenopelmatini) were not recovered as monophyletic (part 5 of Fig. 117).

Previous studies have questioned the monophyly of Ctenopelmatinae. Gauld and Wahl (2006) stated that it is possible that Ctenopelmatinae may represent a basal grade within Ophioniformes. Our total-evidence parsimony analyses did not support this hypothesis, but the subfamily's paraphyly with respect to many other small subfamilies and the lack of resolution of most of the ctenopelmatine tribes agrees with the conclusions of Gauld et al. (1997) who stated that the classification of the group is the least satisfactory of any ichneumonid subfamily. Belshaw and Quicke (2002) using the 28S D2–D3 region found that their five ctenopelmatine exemplars were paraphyletic with respect to *Mesochorus* sp. (Mesochorinae) and *Colpotrochia cincta* (Scopoli) (Metopiinae). The much more extensive analysis of Quicke et al. (2009) found Tryphoninae as the sister group to a grade of Ctenopelmatinae leading to the rest of Ophioniformes. The position of the various Ctenopelmatinae groupings relative to themselves and the other Ophioniformes subfamilies varied greatly, depending on whether gaps were treated as informative or not. Based on the current and previous studies, is there a way forward to create a natural classification of the Ctenopelmatinae and related taxa?

Our total-evidence analyses indicate that the taxa currently comprising Ctenopelmatinae belong within Ophioniformes and yet not within the “higher Ophioniformes” (Anomaloninae, Campopleginae, Cremastinae, Nesomesochorinae, Ophioninae). Ctenopelmatinae may be related to Mesochorinae (part 4 of Fig. 117), (perhaps mesochorines could even be derived from within it) (part 1 of Fig. 120) and several small superfamilies may also need to be placed within it (e.g., Tatogastrinae, Oxytorinae) (part 5 of Fig. 117). It may be related to Metopiinae (part 1 of Fig. 120), or it may not (part 4 of Fig. 117). Beyond this, the subfamily is not defined by any morphological synapomorphy. Taxa in several other subfamilies have the fore tibial tooth including Mesochorinae (Gauld and Wahl 2006), Sisyrastolinae (Bennett et al. 2013) and some Tryphoninae (Bennett 2015), and the distinctiveness of the tooth varies within Ctenopelmatinae. The 28S D2–D3 gene by itself does not seem to provide clear resolution of this part of the ichneumonid phylogeny, as evidenced by the major differences in arrangement of ctenopelmatines based on differing gap treatments and costs in Quicke et al. (2009). Addition of COI barcoding region and EF1a in the current study may have helped us find molecular characters to support Ctenopelmatinae (including some of the small subfamilies), but the results of our total-evidence parsimony analysis may have also been affected by our relatively low number of exemplar ctenopelmatines. It is possible that adding more exemplar species may create instability in the topology as was seen in Quicke et al. (2009). In terms of monophyly of the tribes of Ctenopelmatinae, we think it likely that their monophyly in some of the analyses of Quicke et al. (2009) was an artefact of the coding of morphology at the tribal level for Ctenopelmatinae. The major differences in topology among our five analyses and previous studies corroborate Gauld et al. (1997) that internal relationships of Ctenopelmatinae and relationships of these taxa to other subfamilies are one of the least clearly resolved parts of the ichneumonid phylogeny.

Cylloceriinae

In the total-evidence parsimony analysis, Cylloceriinae (*Cylloceria melancholica*) was sister taxon to *Spilopteron occiputale* (Acaenitinae) in the middle of our Pimpliformes grouping (part 2 of Fig. 117). This relationship was supported by 22 synapomorphies, of which only one was morphological: character 13, state 1: occiput with medial notch present near foramen magnum, a trait evolved independently in *Poemenia albipes* (Cresson) (Poemeniinae), *Coleocentrus rufus* (Acaenitinae) and a clade containing most of Pimplinae. The Bremer support value was 9. The morphology-only parsimony analysis had *C. melancholica* as sister to *Diacritus incompletus* (Diacritinae) with these two species sister group to Acaenitinae (part 1 of Fig. 118). There were only three characters supporting *C. melancholica* + *D. incompletus* and the Bremer support value was only 1. Conversely, the molecular-only parsimony analysis supported a grouping of *C. melancholica* + *Theronia bicincta* (Cresson) (Pimplinae), based on 14 substitutions (part 2 of Fig. 119). In the total-evidence Bayesian analysis, *C. melancholica* was in a clade that lacked resolution with *S. occiputale*, *D. incompletus* and (*Coleocentrus rufus* + *Collyria catoptron*). The support for this grouping was low (BPP = 75). The Bayesian analysis with only molecular characters placed *C. melancholica* within Pimpliformes,

but the relationships at the base of this clade lacked resolution with low posterior probabilities (part 2 of Fig. 121).

Wahl and Gauld (1998) found the following relationship based on a morphological parsimony analysis: Acaenitinae + (Diacritinae + (Cylloceriinae + (Diplazontinae + Orthocentrinae)). The grouping of Cylloceriinae + (Diplazontinae + Orthocentrinae) makes sense biologically because all species for which hosts are known are endophagous in Diptera (Wahl 1990). It was expected that our morphology-only parsimony analysis would find the same results as Wahl and Gauld (1998), but their study coded Acaenitinae and Diplazontinae at subfamily level and their character set was designed specifically to analyze Pimpliformes, not all of Ichneumonidae. It should be noted that when we analyzed only the morphological characters with a Bayesian approach, we found the following: Cylloceriinae + (a grade of Orthocentrinae + Diplazontinae), but with a posterior probability of only 69 (results not shown). More recently, most of the analyses of Klopstein et al. (2019) found that Cylloceriinae formed a clade with Orthocentrinae and Diacritinae.

The combined analyses of Quicke et al. (2009) generally recovered Diacritinae + (the acaenitinae *Procinetus* + ((higher Pimpliformes) + (other Acaenitinae + (Cylloceriinae + (Orthocentrinae + (Diplazontinae + (Collyriinae + *Hyperacmus*))))). As exemplars of Cylloceriinae, Quicke et al. (2009) included two species of *Cylloceria* and *Allomacrus arcticus* (Holmgren) and these species clustered together. They did not include any species of *Rossemia* Humala. Most of their analyses (including both cladograms they provide) recovered a sister-group relationship of *Hyperacmus* with Collyriinae, not Cylloceriinae. Only when high gap costs were applied (not shown) did *Hyperacmus* cluster with Cylloceriinae. Nevertheless, Quicke et al. (2009) formally transferred *Hyperacmus* to Cylloceriinae. One of their rationales for this move was based on the fact that the venom reservoir of *Cylloceria* and *Hyperacmus* possess the uniquely derived state of being comprised of two symmetric parts. In addition, Quicke et al. (2009) point out that the venation of the two genera is similar, males of both have concave tyloids on rather basal flagellomeres, and the propodeum is elongated with strong latero-median carinae (shared characters also summarized by Broad et al. 2018). Alternate placements for *Hyperacmus* include Orthocentrinae (Wahl and Gauld 1998) and related to *Microleptes* (Humala 2003). Unfortunately, we were not able to include sequence of *Hyperacmus* in the current study. In addition, the larva of *Hyperacmus* is not known and this knowledge would be instructive in confirming the placement of *Hyperacmus*. We were also not able to include specimens of *Rossemia* or *Allomacrus* Förster.

In our study, all the exemplars of Diacritinae, Acaenitinae, Collyriinae, Cylloceriinae, Diplazontinae and Orthocentrinae clustered together in only one analysis: the total-evidence Bayesian analysis (part 1 of Fig. 120) and only with weak support (BPP = 89). Neither of our total-evidence analyses recovered the relationship of Cylloceriinae with Orthocentrinae, Diplazontinae and Collyriinae, but this may have partly been because of the aberrant 28S sequence of *S. occiputale* which may have affected relationships in this region of the tree (see Acaenitinae, above). In summary, our analyses unequivocally confirm previous results that *Cylloceria* belongs to Pimpliformes (Wahl

and Gauld 1998; Quicke et al. 2009). Its precise placement within Pimpliformes is uncertain and depends on the characters used and the type of analysis, but it certainly appears more likely to be related to Acaenitinae, Collyriinae, Diacritinae, Diplazontinae and Orthocentrinae, as opposed to the higher Pimpliformes.

Diacritinae

The total-evidence parsimony analysis recovered our single exemplar of Diacritinae (*Diacritus incompletus*) in a clade within Pimpliformes with equivocal relationships as follows: *Diacritus/ Coleocentrus rufus + Collyria catoptron/* all species of Pimplinae, Poemeniinae and Rhyssinae (part 2 of Fig. 117). This clade was supported by 15 synapomorphies, of which 5 were morphological, and a Bremer support value of only 1. See the section on Cyloceeriinae (above) for more description of the placement of Diacritinae in our analyses.

Previous analyses have found Diacritinae as either sister to all Pimpliformes (Quicke et al. 2009), to all Pimpliformes except for Acaenitinae (Wahl and Gauld 1998), or related to Orthocentrinae and Cyloceeriinae (Klopfstein et al. 2019). Our conclusions about the placement of Diacritinae are similar to that of Cyloceeriinae: it most likely belongs to the grouping with Acaenitinae, Collyriinae, Cyloceeriinae, Diplazontinae and Orthocentrinae, but the current study does not clarify its relationships within this group. Nothing is known of the biology or larva of any of the three included genera and this information could help to place Diacritinae more precisely.

Diplazontinae

The monophyly of Diplazontinae (*Diplazon laetatorius* (Fabricius) and *Woldstedtius flavolineatus* (Gravenhorst)) was supported in all of our analyses, regardless of the data used or the method of analysis (Table 3). In the total-evidence parsimony analysis (part 2 of Fig. 117), Diplazontinae was supported by 43 synapomorphies including 16 morphological of which 3 were uniquely derived: 5(4) mandibles tridentate (Fig. 16); 107(1) larval pleurostoma and mandible location shifted ventrally inferior to mandibular process opposite labial palpus (Fig. 100); and 126(1) larval labial sclerite with ventral margin produced as a spine (Fig. 100). The Bremer support value was more than 10 steps.

As described above in the section on Cyloceeriinae, all previous studies have placed Diplazontinae within Pimpliformes, generally as sister group to Orthocentrinae (Gauld and Wahl 1998; Quicke et al. 2009). Our total-evidence parsimony analysis did not support this grouping as the arrangement of Pimpliformes was “upside-down” (with Diplazontinae as sister group to all other taxa) similar to the transcriptome and maximum likelihood anchored enrichment analyses of Klopfstein et al. (2019). The current Bayesian total-evidence analysis did recover the three species of Orthocentrinae in a clade with Diplazontinae, but Orthocentrinae formed a grade leading to Diplazontinae and support for the grouping was low (BPP = 76) (part 2 of Fig. 120). The generic relationships of Diplazontinae are relatively well-studied on the basis of a phylogenetic analysis using morphological characters and four genes (Klopfstein et al. 2011) as are the species concepts (e.g., Dasch 1964; Klopfstein 2014).

Eucerotinae

As described in the section above on Agriotypinae, in the total-evidence parsimony analysis part 3 of (Fig. 117), *Euceros* sp. nov. was sister taxon to *Agriotypus armatus*, these two taxa being sister group to the remainder of Ichneumoniformes sensu lato except for ((Claseinae + Pedunculinae) + (Brachycyrtinae + Labeninae)). This was similar to the molecular-only parsimony analysis except that *Euceros* sp. nov. was in a clade as follows: (*Agriotypus armatus* + (*Brachycyrtus wardae* + *Euceros* sp. nov.)) (part 2 of Fig. 119). *Euceros* sp. nov. occupied a similar position in both Bayesian analyses: close to *A. armatus* and near the base of Ichneumoniformes s.l. except for Labeninae, Brachycyrtinae and related subfamilies (part 2 of Fig. 120, part 2 of Fig. 121). The only different hypothesized relationship for *Euceros* sp. nov. was in our morphology-only parsimony analysis in which *Euceros* sp. nov. was sister to *Neorhacodes enslini* (Neorhacodinae) with 18 synapomorphies of which 4 of them were uniquely derived, although all of the uniquely derived character states described the egg and biology of *Euceros* sp. nov. with reversals/ transformations in *N. enslini* (part 2 of Fig. 118). Optimization of these characters using DELTRAN changed these four characters to be autapomorphies of *Euceros* sp. nov. There was no resolution in this part of the tree to be able to determine relationships of this pairing.

Euceros Gravenhorst is unique in Ichneumonidae in that species lay eggs on vegetation which hatch into planidial larvae (Tripp 1961). It has previously had an uncertain placement in Ichneumonidae. Viereck (1918) included *Euceros* within his Ctenopelminae (*Ctenopelma* Holmgren, etc.), but later (Viereck 1919) raised the taxon to subfamily status as “Eucerinae”. Townes (1945) placed it as a tribe within Ctenopelmatinae, but later as a tribe in Tryphoninae (Townes et al. 1965, Townes 1969). Short (1959) placed *Euceros* as a tribe (Euceratini) in Ctenopelmatinae. Perkins (1959a) reverted the rank of *Euceros* to a subfamily (“Euceratinae”) and Short (1978) concurred with this placement on the basis of larval characters. It is now recognized that the apparent similarities between *Euceros*, Tryphoninae and Ctenopelmatinae are based on symplesiomorphies such as the non-petiolate T1 (character 76, state 0) with spiracle placed anterior to middle (character 77, state 0) (Fig. 72). Furthermore, it is not believed that the stalked egg of Tryphoninae (Fig. 113) is homologous to the stalked egg of Eucerotinae (Figs 115–116) (Gauld and Wahl (2002). The egg in Tryphoninae is an extension of the chorion (Kasparyan 1973); whereas, the stalk of *Euceros* is a secretion that hardens allowing the egg to be stuck to vegetation (Tripp 1961).

Previous phylogenetic studies have attempted to ascertain the relationships of Eucerotinae within Ichneumonidae. A morphological analysis by Gauld and Wahl (2002), using a limited number of outgroups, found that Eucerotinae was sister group to *Labium* (Labeninae) + *Brachycyrtus*. The combined morphological and molecular studies of Quicke et al. (2000a) (using 28S D2) and Quicke et al. (2009) (using 28S D2–D3) generally found that *Euceros* was sister to *Brachycyrtus* with this pairing often associated with Claseinae, Pedunculinae, and Microleptinae within Ichneumoniformes s.l. except Labeninae. Similar results were found by Santos (2017) with seven genes and morphology. Overall, our analyses generally concur with the findings of Quicke et al.

(2009) and Santos (2017) that *Euceros* is placed near the base of Ichneumoniformes s.l. There are no morphological characters that support this placement and the unique biology of *Euceros* also offers no clues as to whether it is correct.

Hybrizontinae

Hybrizon rileyi, the exemplar of Hybrizontinae in our study, was sister to *Lycorina glaucomata* (Lycorininae) in the total-evidence parsimony analysis and was nested within the Ctenopelmatinae and relatives clade (part 5 of Fig. 117). The pairing was supported by 41 synapomorphies, of which 6 were morphological with a Bremer support value of 7 steps. None of the morphological characters supporting this pair were uniquely derived or even had a consistency index above 0.2. The total-evidence Bayesian analysis was similar to the total-evidence parsimony analysis: *H. rileyi* was within the Ctenopelmatinae and relatives clade in a region with equivocal relationships: Perilissini/ (*Rhorus bartelti* Luhman + Ctenopelmatinae Genus NZ/ (*Westwoodia* sp. + (*Onarion* sp. + *H. rileyi*))) (part 1 of Fig. 120). The support for this clade was only 84 and *H. rileyi* had an extremely long branch length. The molecular-only parsimony analysis recovered *H. rileyi* in a clade as follows: (Labeninae + (*Brachyscleroma* sp. + *Aplomerus* sp.) + (Tersilochinae s.s. + (*Mesochorus* sp. + (*Onarion* sp. + *H. rileyi*)))) (part 2 of Fig. 119). Finally, the molecular-only Bayesian analysis placed *H. rileyi* in a similar position to the molecular-only parsimony analysis: not clustering with most members of Ctenopelmatinae, but rather unresolved with members of Tersilochinae, Mesochorinae, Sisyrotolinae and Cremastinae at the base of a clade containing Pimpliformes and members of Ichneumoniformes s.l. (part 1 of Fig. 121).

Similar to *Agriotypus*, *Hybrizon* Fallén and its relatives have had a varied placement over time: included in Braconidae (Achterberg 1976), Ichneumonidae (Gauld 1984), or as a family itself: Hybrizontidae or Paxylommatidae (Marsh 1971, 1989). The different family-level placements have been proposed because of wing venation, primarily because of the lack of fore wing vein *2m-cu* (character 51, state 1) (as in Fig. 49) in *Hybrizon*, a character that defines all of Braconidae except *Apozyx* Mason (Sharkey and Wahl 1992). Nevertheless, other ichneumonids lack *2m-cu* (e.g., *Neorhacodes* Hedicke) and the fossil hybrizontine *Tobiasites striatus* Kasparyan possesses this vein (Kasparyan 1988), indicating that presence of the vein may be the ground plan state for the group. Furthermore, Mason (1981) noted that *Hybrizon* does not have fusion of metasomal tergites 2 and 3, therefore excluding it from Braconidae. Currently, it is believed that *Hybrizon* and its relatives are correctly placed within Ichneumonidae as a subfamily (Sharkey and Wahl 1992) and our results support this: *H. rileyi* did not cluster within the outgroups, nor was it ever placed as sister to the rest of Ichneumonidae.

In terms of proposed placement within Ichneumonidae, Sharkey and Wahl (1992) suggested that on the basis of the lack of vein *2m-cu* and similar host biology (endoparasitoids of Aculeata), Hybrizontinae may be the sister of Neorhacodinae. *Hybrizon* spp. are known to parasitize ants (Donisthorpe 1913, Gómez Durán and Achterberg 2011), whereas *Neorhacodes* spp. parasitize stem-nesting Crabronidae (Horstmann 1968; Danks 1971). None of our results support this relationship. More recent studies

using sequence data and morphology (Quicke et al. 2009) often recovered a relationship of *Hybrizon* with *Lycorina* Holmgren (Lycorininae), but that study stated that the placement of *Hybrizon* was highly variable depending on the analysis (although generally related to Ophioniformes taxa). In the end, Quicke et al. (2009) suggested that *Hybrizon* may be a derived Anomaloninae. In summary, our combined analyses suggest Hybrizontinae may be related to Ctenopelmatinae, whereas our molecular-only analyses place it somewhere within Ophioniformes (but not the higher Ophioniformes). Certainly its biology does not lend support to the notion that it is a ctenopelmatine which are mostly parasitoids of sawflies, but neither does it suggest it is an anomalonine, which parasitize Lepidoptera (Gauld et al. 1997).

Ichneumoninae

The following discussion pertains to the 13 exemplar species of Ichneumoninae excluding Alomyini. See the section on Alomyinae (above) for the rationale for moving *Alomya* and *Megalomya* within Ichneumoninae (as Alomyini).

The 13 species of Ichneumoninae were monophyletic in all analyses (Table 3). The total-evidence parsimony analysis had 32 synapomorphies supporting Ichneumoninae, of which 9 were morphological, including the uniquely derived character state 84(1) gastrocoelus present (Fig. 77). The Bremer support value was greater than 10 steps. (Ichneumoninae + *Alomya debellator*) was the sister of Phygadeuontinae in both total-evidence analyses and these were sister group to Cryptinae s.s. As discussed in the discussion of Ichneumoniformes (above), various other taxa were associated with this grouping, including Adelognathinae, Agriotypinae, Brachycyrtinae, Claseinae, Eucerotinae, Microleptinae and Pedunculinae as well as Labeninae in a more distant relationship.

In terms of the tribes, all analyses recovered the two species of Platylabini together (*Cyclolabus impressus* (Provancher) + *Linyctus exhortator* (Fabricius)) and the two species of Heresiarchini (*Coelichneumon eximius* (Stephens) + *Protichneumon grandis* (Brullé)) were also always monophyletic, although the latter pair was always nested within Ichneumonini (5 species), as was the single exemplar of Listrodromini (*Dilopharius otomitus* (Cresson)). All analyses except parsimony with only morphological characters recovered Phaeogenini as monophyletic (*Stenodontus* sp. nov. + (*Centeterus euryptychia* (Ashmead) + *Phaeogenes hebrus* (Cresson))), and (Platylabini + Phaeogenini) was sister to all other species in the total-evidence and molecular-only parsimony analyses (Figs 117, 119).

In terms of tribal relationships, Quicke et al. (2009) summarized their findings by stating that they found Phaeogenini and Platylabini “in basal positions” within Ichneumoninae, although their consensus cladogram with gaps treated as informative had Platylabini in the middle of Ichneumoninae and their analysis with gaps treated as missing data had some members of Phaeogenini separated from the rest and nested within a clade comprised predominantly of Ichneumonini species. More recently, the maximum likelihood total-evidence analysis of Santos (2017) found that all five species of Phaeogenini clustered together as sister group to the other eight Ichneumoninae species, but this same analysis did not recover a monophyletic Platylabini. We accept the hypothesis

supported by the majority of our analyses, that Phaeogenini and Platylabini are sister groups and these two groups form a sister group to the rest of Ichneumoninae except for Alomyini. We do concede that our low taxon sampling may be presenting a simplified view that may not be supported by future studies with additional taxa.

With respect to monophyly and relationships of the other tribes of Ichneumoninae, none of the studies of Laurenne et al. (2006), Quicke et al. (2009), Santos (2017) or our analyses have found support for Heresiarchini relative to Ichneumonini. We did not include any of the morphologically distinct *Callajoppa* group (Sime and Wahl 2002), which would need to be done to study the relationships of Heresiarchini and Ichneumonini further. Sime and Wahl (2002), using morphology alone, recovered Heresiarchini as monophyletic, but only included one non-heresiarchine as an out-group (*Ichneumon caliginosus* Cresson), therefore it could not draw conclusions regarding the monophyly of Heresiarchini relative to Ichneumonini as a whole. In summary, it appears as though more taxa, characters and knowledge of biology will need to be assessed to determine the internal structure of Ichneumoninae.

Labeninae

Labeninae was monophyletic in all analyses except parsimony using only morphology (Table 3). In the total-evidence parsimony analysis, Labeninae was strongly supported by 52 synapomorphies, of which 8 were morphological (none uniquely derived) and a Bremer support value of greater than 10 steps (part 3 of Fig. 117). Labeninae was sister to Brachycyrtinae (Bremer support of 10) and these two subfamilies were sister to (Claseinae + Pedunculinae) (Bremer support of 8). Together these four subfamilies were sister group to all other taxa within Ichneumoniformes s.l. In contrast, neither of the Bayesian analyses recovered a sister-group pairing of Brachycyrtinae and Labeninae but rather, Labeninae was sister group to a clade comprised of the remaining exemplars of Ichneumoniformes s.l. + Pimpliformes (part 2 of Fig. 120, part 2 of Fig. 121). There was low support for this relationship in the total-evidence Bayesian tree (BPP = 66), but strong support in the molecular-only analysis (BPP = 99).

Some previous studies have suggested that Labeninae may be sister group to all ichneumonids except Xoridinae, for example, most analyses in Quicke et al. 2009, the unweighted parsimony analysis of Santos (2017) and two of five anchored enrichment analyses in Klopstein et al. (2019). This placement was not supported by the current results. The latter study found a lack of stability in the placement of Labeninae, for example, their maximum likelihood analysis with amino acids placed Labeninae as sister to Ichneumoniformes s.l. + Pimpliformes, whereas the likelihood analysis analyzing all nucleotides placed Labeninae as sister to Pimpliformes. In terms of the relationship of Labeninae to Brachycyrtinae, Claseinae and Pedunculinae, Quicke et al. (2009) generally recovered the latter three subfamilies as monophyletic but as sister group to the rest of Ichneumoniformes, not Labeninae. This was similar to the maximum likelihood analysis of Santos (2017) who found Labeninae + (Claseinae + (Eucerotinae + Brachycyrtinae)) + (the rest of Ichneumoniformes). Note that both Santos (2017) and Klopstein et al. (2019) only included one species of Labeninae in their analyses. In

summary, with respect to the placement of Labeninae, the current study either found that Labeninae is part of the sister group to Ichneumoniformes s.l. (with Brachycyrtinae, Claseinae and Pedunculinae) or as sister group by itself to a clade comprising Ichneumoniformes s.l. + Pimpliformes. Based on the equivocal placement of Labeninae in the current study, including apparent strong support as sister to Brachycyrtinae in the total-evidence parsimony analysis, we do not currently recognize the higher group Labeniformes of Quicke et al. (2009).

With respect to tribal relationships within Labeninae, our analysis only included exemplars of three tribes (no Xenothyridini exemplars). In the consensus tree of the total-evidence parsimony analysis, the tribes Labenini (*Labena grallator* (Say) + *Apechoneura* sp.), Orthognathelini (= Groteini) (*Grotea anguina* Cresson + *Labium* sp.) and Poecilocryptini (*Poecilocryptus nigromaculatus*) had equivocal relationships (part 3 of Fig. 117). The Bayesian analyses both supported the following topology: (Orthognathelini + (Poecilocryptini + Labenini)) which is the same as the hypothesis of Gauld and Wahl (2000). This topology contradicts the relationships hypothesized by Wahl (1993a) and Quicke et al. (2009): Poecilocryptini + (Orthognathelini + Labenini).

Lycorininae

The placement of Lycorininae (*Lycorina glaucomata*) was one of the least stable of any taxon in our analyses. The total-evidence parsimony analysis placed *L. glaucomata* within the clade of Ctenopelmatinae and relatives as sister to Hybrizontinae (see section on Hybrizontinae for details on support). In the parsimony analysis with only molecular characters, *L. glaucomata* was sister to the rest of Ichneumonidae (part 1 of Fig. 119), and in the two Bayesian analyses it was placed within a grade along with *Neorhacodes enslini* (Neorhacodinae) and various exemplars of Tryphoninae (part 1 of Fig. 120, part 1 of Fig. 121).

Quicke et al. (2009) also found inconsistent placement of Lycorininae, including: 1) sister group to Hybrizontinae; 2) grouping with *Townesion* Kasparyan (Banchinae: Glyptini), and with these two taxa as sister group to the rest of Banchinae; and 3) grouping with Tersilochinae s.l. as sister group to Banchinae. They dismissed the association of Lycorininae with Hybrizontinae as “long-branch attraction”, but did point to the presence of an aulaciform rod of the ovipositor (see Quicke et al. 1994) as evidence that Lycorininae belong to Ophioniformes.

What is known of the biology of *Lycorina* is that they are koinobionts (Coronado-Rivera et al. 2004) that oviposit in the anus of Lepidoptera larvae and complete development externally on the host and pupate inside the host cocoon (Shaw 2004) (our character 138(2)). The egg of *Lycorina* is stalked with an anchor, similar to most Tryphoninae, but Coronado-Rivera et al. (2004) note three differences between the eggs and method of oviposition. First, lycorinine eggs are much narrower than eggs of Tryphoninae (0.3 mm average width (for 10 species in 5 tribes) versus 0.1 mm for two species of *Lycorina*). Second, during oviposition, the stalk and/or anchor of almost all tryphonine eggs travel down the ovipositor while the body of the egg exits the female from the genital opening at the base of the ovipositor (character 136(1)). This process

was not witnessed in Lycoriniinae (Shaw 2004), and it is therefore likely that the entire egg travels down the ovipositor (character 136(0)). Third, the eggs of Tryphoninae have a more strongly sclerotized chorion than Lycoriniinae. Whereas our two Bayesian analyses placed *L. glaucomata* near Tryphoninae, Lycoriniinae was never nested within Tryphoninae, which agrees with the findings of Quicke et al. (2009). The current study and Quicke et al. (2009) therefore support the hypothesis that the stalked eggs of Lycoriniinae and Tryphoninae have evolved independently.

In summary, the majority of our analyses agreed with Quicke et al. (2009) that Lycoriniinae is related to Ophioniformes. Our total-evidence parsimony analysis suggested a relationship with Ctenopelmatinae, whereas Townes (1970b) and Quicke et al. (2009) support a relationship with Banchinae.

Mesochorinae

The five species of Mesochorinae only clustered together in the morphology-only parsimony analysis (part 3 of Fig. 118) based on 15 synapomorphies, of which one was uniquely derived: character 140(9): oviposition into host inside host (i.e., internal hyperparasitoid). In both Bayesian analyses and the total-evidence parsimony analysis, only four of the five mesochorine species clustered together, with *Chineater masneri* consistently paired with *Scolomus* sp. (Metopiinae) and associated with *Tatogaster nigra* (Tatogastrinae) and various ctenopelmatine species. *Chineater masneri* has not been included in a phylogenetic analysis since the morphological analysis of Wahl (1993b) when it was described, but the latter study included a generalized outgroup, thus forcing monophyly of Mesochorinae (including *C. masneri*). The current study suggests that it may be misplaced in Mesochorinae.

Chineater masneri does have a large, rhombic areolet (character 54(1)) (Fig. 52), which is characteristic of most mesochorines (although obliquely quadrangular in *Cidaphus panisoides* (Ashmead)). A large, rhombic areolet is rare in Ctenopelmatinae (generally the areolet is obliquely quadrangular or open). The ovipositor of *C. masneri* is thin and needle-like (character 99(2)) (Fig. 85) as in all mesochorines, but it is relatively short for a mesochorine. Most ctenopelmatines have a dorsal, subapical notch on the ovipositor, but a thin, needle-like ovipositor is known in most Pionini (e.g., *Rhorus bartelti*) as well as some Perilissini and Ctenopelmatini, therefore this character does not help in the subfamily placement of *C. masneri*. As discussed under Ctenopelmatinae, the apical tooth of the fore tibia (character 68(1)) is not diagnostic of Ctenopelmatinae by itself and, in fact, this character state is present in all five of our mesochorine species, including *C. masneri*. What may help decide the placement of *C. masneri* would be knowledge of either: a) the male gonoforceps – if rod-like (character 102(1)), then this would support placement in Mesochorinae, or; b) oviposition location – if an internal hyperparasitoid (character 140(9)), then this would also support the hypothesis that *C. masneri* is correctly placed in Mesochorinae. Until one or both of these characters are known, we defer transfer of *Chineater* and maintain it within Mesochorinae.

With respect to the four other mesochorine species, the total-evidence parsimony analysis placed them in a clade with equivocal relationships within Ophioniformes as

follows: Mesochorinae except *Chineater*/ Ctenopelmatinae and relatives/ Metopiinae to Campopleginae (part 4 of Fig. 117). The clade “Mesochorinae except *Chineater*” was supported by 45 synapomorphies, of which 9 were morphological, including the uniquely derived character 140(9): oviposition into a host inside a host. The Bremer support was 10+ steps. Our Bayesian total-evidence analysis had a similar placement for the group (Mesochorinae except *Chineater*): related to a clade containing ((Ctenopelmatinae and relatives including Metopiinae) + the higher Ophioniformes) (part 1 of Fig. 120). In terms of relationships within Mesochorinae, in the total-evidence parsimony analysis, *Mesochorus* sp. was sister to the other three exemplars (*Astiphromma* sp. nov., *Cidaphus paniscoides* and *Lepidura collaris* Townes) that had equivocal relationships. This arrangement contradicts Wahl (1993b) who found that *Cidaphus* Förster was sister group to all other genera. The Bayesian total-evidence analysis favoured *C. paniscoides* as the sister to the other three species, but only with weak support (BPP = 69).

There have been some previous studies that suggested that Mesochorinae may render Ctenopelmatinae paraphyletic (Belshaw and Quicke 2002; Quicke et al. 2009), but this hypothesis was not supported in any of our five analyses. Neither was the hypothesis of Quicke et al. (2009) that *Tatogaster nigra* Townes (Tatogastrinae) belongs to Mesochorinae. Owing to the lack of resolution of natural groups within Ctenopelmatinae, future phylogenetic studies including Ctenopelmatinae, Mesochorinae, Metopiinae and Tatogastrinae are definitely warranted which will hopefully clarify the placement of Mesochorinae.

Metopiinae

Similar to Mesochorinae, all four species of Metopiinae only clustered together in the morphology-only parsimony analysis (part 3 of Fig. 118), supported by 20 synapomorphies (none uniquely derived) and a Bremer support of 2. In the other analyses, three of the four species (*Exochus semirufus* Cresson, *Metopius pollinctorius* (Say) and *Seticornuta terminalis* (Ashmead)) shared a common ancestor with strong support (Table 3), but *Scolomus* sp. was placed elsewhere within Ophioniformes. In the total-evidence parsimony analysis, the three Metopiinae species that clustered together were supported by 46 synapomorphies, including 17 morphological (none uniquely derived), and a Bremer support of greater than 10 steps (part 6 of Fig. 117). Metopiinae (except *Scolomus* sp.) was the sister group to (*Stilbops vetulus* + the unresolved clade (*Notostilbops* sp. nov./ *Lissonota scutellaris* + *Exetastes bioculatus*/ Glyptini)). See sections on Banchinae and Stilbopinae for further description of these relationships. Together this grouping was the sister group to the higher Ophioniformes. In contrast, the total-evidence Bayesian analysis placed Metopiinae (except *Scolomus* sp.) in an unresolved clade as follows: Metopiinae (except *Scolomus*)/ *Ctenopelma sanguineum* (Provancher)/ (*Tatogaster nigra* + (*Chineater masneri* + *Scolomus* sp.)) and a cluster of six Ctenopelmatinae (part 1 of Fig. 120). This grouping was, however, very weakly supported (BPP = 71). Based on the support values of this part of the tree, the Bayesian analysis only tells us that Metopiinae belongs to Ophioniformes, but not within the higher Ophioniformes.

Gauld and Wahl (2006) suggested that Metopiinae may have arisen from within Ctenopelmatinae. Our total-evidence parsimony analysis refuted this hypothesis, but our Bayesian total-evidence analysis had some weak support for the relationship, albeit with a general lack of resolution in this part of the tree. In summary, the most well-resolved hypothesis of the placement of Metopiinae from the current study is that it is related to Stilbopinae and Banchinae, in contrast to the hypothesis of Gauld and Wahl (2006) and the results of Quicke et al. (2009). Biologically, Metopiinae, Stilbopinae and Banchinae share parasitism of Lepidoptera (Wahl 1993c) which is much less common in Ctenopelmatinae – a few Holarctic species of *Lathrolestes* Förster have been reared from Eriocraniidae (Heath 1961) and some species of *Megaceria* Szépligeti in Australia parasitize Geometridae (Morley 1913) and Notodontidae (Gauld 1984).

In terms of the placement of *Scolomus*, Gauld and Wahl (2006) synonymized the metopiine genus *Apolophus* Townes, 1971 with the ctenopelmatine genus *Scolomus* (tribe Pionini) with the name *Scolomus* Townes & Townes, 1950 having priority. Because the morphological evidence supporting placement in either subfamily was equivocal, they placed *Scolomus* within Metopiinae on the basis of the one host record for *Scolomus*: *S. borealis* (Townes) reared from *Schrekensteinia festaliella* (Hübner) (Lepidoptera: Schrekensteiniidae) (Broad and Shaw 2005). Quicke et al. (2009) stated that the placement of *Scolomus* was “associated with various Ctenopelmatinae” and in only a few analyses was it recovered as sister to Metopiinae. On the basis of all of our analyses except parsimony (morphology-only), the species of *Scolomus* that we included in our analysis does not seem to be well-placed with our other exemplars of Metopiinae. But where is it best placed?

The current total-evidence parsimony analysis placed *Scolomus* within the Ctenopelmatinae and relatives grouping (part 5 of Fig. 117) and not closely related to the other three Metopiinae species. The total-evidence Bayesian analysis was less clear as *Scolomus* was placed in a clade that included the three other metopiine species and seven ctenopelmatines (part 1 of Fig. 120), but with low support (BPP = 71). Whereas it is tempting to suggest that *Scolomus* should be moved to Ctenopelmatinae on the basis of the parsimony total-evidence results, the fact that the analyses are placing it next to several other enigmatic taxa makes this decision difficult, especially with respect to the decision of which ctenopelmatine tribe it should be placed. It is also possible that the synonymy of *Scolomus* and *Apolophus* by Gauld and Wahl (2006) was not correct. Our exemplar specimen would have been placed in *Apolophus* prior to 2006 on the basis of the lack of horns on the subtegular ridge. Prior to any decision on the subfamily placement of *Scolomus*, it would be prudent to undertake a revision of the genus (including description of new species that may be intermediate between *S. borealis* and *S. viridis* Townes & Townes) in order to confirm its monophyly. For now, we delay a decision on the placement of *Scolomus* until this work has been completed.

Unfortunately, we were not able to include any other of the problematic genera of Metopiinae in our analysis: *Bremiella* Dalla Torre, *Ischyrocnemis* Holmgren, and *Lapton* Nees; therefore we cannot comment on their relatedness to the four exemplar metopiines we analyzed. Quicke et al. (2009) found their placements unstable, but stated that

Ischyrocnemis was consistently recovered within Pimpliformes, *Bremiella* sometimes was a sister group to Metopiinae or associated with various Ctenopelmatinae and *Lap-ton* was sometimes recovered with a grouping including Ophioninae, Campopleginae, Anomaloninae and Mesochorinae.

Microleptinae

Microleptinae (*Microleptes* sp.) was sister to *Ateleute* sp. nov. (Ateleutinae) in the parsimony total-evidence analysis, supported by 37 synapomorphies (7 morphological, none of which were uniquely derived) and a Bremer support of 6. These two taxa were sister group of (Cryptinae + (Phygadeuontinae + (Alomyinae + Ichneumoninae))) (part 3 of Fig. 117). The Bayesian total-evidence analysis was similar, with *Microleptes* sp. in a well-supported clade (BPP = 98) that lacked internal resolution, but included (*Adelognathus* sp. + *Ateleute* sp.) and (Cryptinae + (Phygadeuontinae + (Alomyinae + Ichneumoninae))) (part 2 of Fig. 120).

Previous studies were equivocal in their placement of Microleptinae. Wahl (1986) described the larva stating that the reduced hypostomal spur, shape of the stipital sclerite and small size of the labial sclerite was similar to the larvae of Metopiinae and Anomaloninae (Ophioniformes), but stated that these similarities may be convergences based on similar larval behaviour (spinning flimsy cocoons inside the host pupa). The morphological character analysis in Quicke et al. (2000a) placed Microleptinae in a clade with Orthocentrinae and Diplazontinae (Pimpliformes) which is consistent with their biology as endoparasitoids of Diptera larva (*Microleptes* has been reared from Stratiomyidae: Wahl 1986). The combined morphology and 28S D2–D3 sequence analysis of Quicke et al. (2009) suggested that Microleptinae belonged to Ophioniformes as sister group to Orthopelmatinae, with these two taxa being the sister group to either Tersilochinae (gaps treated as missing) or (when gaps treated as informative), nested within Ctenopelmatinae in a clade as follows: Perilissini + (Oxytorinae + (Seleucini + (Microleptinae + Orthopelmatinae)). Conversely, the molecular-only analysis of Quicke et al. (2009) placed Microleptinae as sister group to Eucerotinae near the base of the Ichneumoniformes (close to the placement of the current study). Santos (2017) also recovered *Microleptes* within Ichneumoniformes, its precise placement dependent on the method of analysis (parsimony versus maximum likelihood).

Our study provides support for the placement of Microleptinae near the base of Ichneumoniformes s.l. In terms of morphology, there are no compelling characters for this placement – the only uniquely derived character in this region of the tree is Character 9 (state 1): central flagellomeres of male with elliptical or longitudinal ridge-like tyloids which supports Adelognathinae + ((Microleptinae + Ateleutinae) + (Cryptinae + (Phygadeuontinae + (Alomyinae + Ichneumoninae))))). This character; however, has a reversal in Microleptinae + Ateleutinae (part 3 of Fig. 117). The support, therefore, comes mainly from the molecular characters. Both of our total-evidence analyses and both of our analyses with only molecular characters supported the monophyly of the seven subfamilies listed directly above (e.g., BPP of 100 in Bayesian analysis with only molecular characters) (part 2 of Fig. 121).

Neorhacodinae

Neorhacodinae (*Neorhacodes enslini*) was perhaps the most unstable taxon in our analyses. The total-evidence parsimony analysis placed *N. enslini* within Tryphoninae (as sister to Phytodietini) (part 4 of Fig. 117). The parsimony analysis with only molecular characters placed *N. enslini* as sister to all Ichneumonidae except *Lycorina glaucomata* (Lycorininae) (part 1 of Fig. 119) and the two Bayesian analyses were similar, except that *Neorhacodes enslini* was sister to all other Ichneumonidae (part 1 of Fig. 120, part 1 of Fig. 121).

Originally, Ruschka (1922) described *Rhacodes* Ruschka in its own subfamily in Braconidae. Hedicke (1922) noted that *Rhacodes* was preoccupied by the crustacean *Rhacodes* Koch and renamed the taxon *Neorhacodes* Hedicke, changing the subfamily name to Neorhacodinae. The reason why it was placed within Braconidae is the apparent lack of vein *2m-cu* of the fore wing. Roman (1923) using reflected light concluded that vein *2m-cu* was present and therefore moved *Neorhacodes* to Ichneumonidae, placing it within Pimplinae. Cushman (1940) described a second genus (*Romaniella* Cushman). Townes (1945) listed *Neorhacodes* under “genera of uncertain subfamily” before moving it to Banchinae as a tribe (Neorhacodini) (Townes and Townes 1951). Townes (1971) later raised Neorhacodini to subfamily status “placed between the Lycorininae and the Banchinae”. More recently, Quicke et al. (2009) found that *Neorhacodes enslini* clustered with exemplars of Tersilochinae and the “*Phrudus* group” of Phrudinae and subsequently formally synonymized Neorhacodinae (and the *Phrudus* group) within Tersilochinae. Finally, Broad (2016) considered Neorhacodinae as a separate subfamily, rather than a synonym of Tersilochinae.

Given the equivocal placement of *Neorhacodes enslini* in the current study, we are not able to make any precise statements with respect to the relationships of Neorhacodinae. There are no compelling morphological or biological characters in our study that link Neorhacodinae to Tryphoninae. The egg of Neorhacodinae is not known, and determining whether it bears a stalk or not would help greatly in determining whether the sister-group relationship of Neorhacodinae and Phytodietini is artefactual or not. The current study coded the host of Neorhacodinae as Hymenoptera, which is similar to most Tryphoninae, although Phytodietini are parasitoids of Lepidoptera. Furthermore, one could argue that coding the hosts for *Neorhacodes* (aculeate Hymenoptera) (Horstmann 1968; Danks 1971) the same state as for most Tryphoninae (sawflies) (Kasparyan 1973; Bennett 2015) is not correct and they should be given different states for this character. Similarly, there was no evidence of a close relationship with *Neorhacodes* and Banchinae (as proposed by Townes and Townes 1951), Lycorininae (Townes 1971) or Tersilochinae (Quicke et al. 2009). The most precise statement of affinity that we can make for Neorhacodinae is that it appears to belong *incertae sedis* within Ophioniformes because *N. enslini* was most often associated with taxa belonging to Ophioniformes, and never clustered within Pimpliformes or Ichneumoniformes in our analyses.

Nesomesochorinae

Nesomesochorinae (*Nonnus* sp. and *Chriodes* sp.) was only recovered as monophyletic in the total-evidence parsimony analysis (part 6 of Fig. 117) (Table 3). It was sup-

ported by 31 synapomorphies (6 morphological) and a Bremer support of 2. Character 16 (reduction of maxillary palpomeres from 5 to 4) is a relatively rare synapomorphy in our data set (C.I. = 0.33) and therefore is a good character state supporting the monophyly of these two taxa. Having said this, the parsimony analysis with only morphological characters did not recover these two taxa together: *Chriodes* sp. was placed in the higher Ophioniformes (part 3 of Fig. 118), but the placement of *Nonnus* sp. was not clearly resolved (part 1 of Fig. 118). The other three analyses all had *Nonnus* sp. and *Chriodes* sp. clustering near each other along with the exemplars of Anomaloninae and Ophioninae, although *Nonnus* sp. and *Chriodes* sp. were never sister taxa to each other. In terms of their placement within Ichneumonidae, both total-evidence analyses placed *Nonnus* sp. and *Chriodes* sp. within the higher Ophioniformes (part 6 of Fig. 117; part 1 of Fig. 120) (posterior probability of 98 in the Bayesian tree). The relationships of Nesomesochorinae within the higher Ophioniformes were not precisely clear in the parsimony total-evidence analysis because this group was unresolved as follows: Nesomesochorinae/ Anomaloninae + Ophioninae/ Cremastinae + Campopleginae. Similarly, the Bayesian total-evidence analysis does not help resolve their placement, as they were placed as follows: (*Chriodes* sp. + ((*Nonnus* sp. + Anomaloninae) + Ophioninae)), but this clade only had a posterior probability of 61. All that is suggested by the Bayesian analysis is that *Chriodes* sp. and *Nonnus* sp. do not cluster within Campopleginae + Cremastinae because the sister-group relationship of these two subfamilies is very strongly supported (BPP = 99) (part 1 of Fig. 120).

Nesomesochorini was proposed by Ashmead (1905) to include *Nesomesochorus* Ashmead (= *Chriodes*). Nonnini was proposed by Townes et al. (1961), comprised of *Nonnus*. Townes (1970b) placed *Nonnus* and *Chriodes* together in Nonnini within Campopleginae. Miah and Bhuiya (2001) and later Quicke et al. (2005) showed that these two genera did not belong to Campopleginae. Quicke et al. (2009) established that they belonged together in one subfamily with the oldest family group name having priority (Nesomesochorinae). In terms of affinity, Quicke et al. (2009) found that Nesomesochorinae belonged to the higher Ophioniformes as either sister group of (Cremastinae + Campopleginae) or sister group of Campopleginae (depending on gap treatment). Our total-evidence analyses do not refute a sister-group relationship of Nesomesochorinae to (Cremastinae + Campopleginae), but the lack of resolution means that other relationships within the higher Ophioniformes are also possible (e.g., Anomaloninae + Ophioninae). Our results do not support a sister-group relationship of Nesomesochorinae + Campopleginae.

Ophioninae

Ophioninae (*Enicospilus flavostigma* Hooker, *Hellwigia obscura*, *Ophion* sp. *Skiapus* sp. and *Thyreodon* sp.) was supported in both total-evidence analyses and the parsimony analysis with only morphological characters (Table 3). The subfamily was supported in the total-evidence parsimony analysis by 32 characters (8 morphological) and a Bremer support of 4. Character 37 (state 1): anterior transverse carina of propodeum forming more or less smooth arc (Fig. 38) was a rare synapomorphy in our study (C.I. = 0.5). In addition, character 121 (1): larval cardo present as a slightly sclerotized oval

(Fig. 104) and character 128 (1): 8 or more sensilla on larval prelabium, both had C.I.s of 0.33; however these characters are not known for *Hellwigia obscura* or *Skiapus* sp. The parsimony analysis with only molecular characters supported Ophioninae except for *Skiapus* sp., which clustered with the nesomesochorines and *Anomalon picticorne*. (Anomaloninae) as the sister group to the other ophionines (part 1 of Fig. 119). The Bayesian analysis with only molecular characters had all five ophionines clustering together, but with a low posterior probability (BPP = 84) (part 1 of Fig. 121).

The monophyly of the majority of the genera of Ophioninae has long been established on the basis of the relatively rare (in Ichneumonidae) fore wing areolet lacking vein *Rs* so that the only cross vein is distad vein *2m-cu* (character 54, state 2) (Fig. 53), along with possession of pectinate claws and presence of hind wing vein *2/Cu* (Gauld 1988b). The inclusion of the genera *Hellwigia* and *Skiapus* within Ophioninae is more equivocal. Quicke et al. (2009) found that *Hellwigia* generally clustered with the other exemplars of Ophioninae, whereas the position of *Skiapus* was unstable – sometimes included within Ophioninae or recovered as the sister taxon to the rest of Ophioninae, or in a minority of analyses, clustering with *Anomalon* Panzer and Hybrizontinae. The majority of our analyses place *Skiapus* and *Hellwigia* within Ophioninae (e.g., in the total-evidence parsimony analysis, *Skiapus* sp. + *Hellwigia obscura* are sister group to the other three exemplars) (part 6 of Fig. 117). Knowledge of the larva of *Skiapus* and *Hellwigia* would provide additional evidence to support or refute this placement.

Orthocentrinae

Orthocentrinae (*Megastylus* sp. nov., *Orthocentrus* sp. and *Proclitus speciosus* Dasch) was only recovered as monophyletic in the parsimony analysis using only morphological characters (part 2 of Fig. 118) (Table 3). Orthocentrinae was supported by 18 morphological characters, of which one was uniquely derived: Character 188, state 3: larval hypostomal-stipital plate reduced to narrow strip (Fig. 106) (this character unknown for *P. speciosus*). See the section on Pimpliformes (above) for a description of the relationships of the orthocentrine species to the rest of Pimpliformes.

Previous definitions of Orthocentrinae have differed depending on whether authors considered *Orthocentrus* Gravenhorst and relatives (the *Orthocentrus* group of genera) to be related to *Helictes* Haliday and relatives (the *Helictes* group of genera). Townes (1971) placed the groups in two separate subfamilies. His Orthocentrinae was comprised of the *Orthocentrus* group and his Microleptinae included the *Helictes* group, although he stated that his Microleptinae was a “wastebasket” group and later studies removed several genera to other subfamilies (e.g., Gupta 1988; Wahl 1990). Wahl (1990), on the basis of larval synapomorphies, joined these two groups together in an expanded Orthocentrinae and stated that Orthocentrinae was closely related to Diplazontinae, both of which belonged to the informal grouping Pimpliformes. The morphological cladistic analysis of Pimpliformes by Wahl and Gauld (1998) supported the fact that the *Orthocentrus* and *Helictes* groups shared a common ancestor which was sister taxon to Diplazontinae. In addition, their analysis supported that Orthocentrinae and Diplazontinae belonged to the following grouping: Acaenitinae + (Diacritinae

+ (Cylloceriinae + (Orthocentrinae + Diplazontinae))). Quicke et al. (2009) also recovered Orthocentrinae as monophyletic (except they removed *Hyperacmus* to Cylloceriinae). In their study, Orthocentrinae had a placement within Pimpliformes as follows: (Acaenitinae except for *Procinetus* + (Cylloceriinae + (Orthocentrinae + (Diplazontinae + (Collyriinae + *Hyperacmus*)))). More recently, Klopstein et al. (2017) found strong support for seven species of Orthocentrinae in their anchored enrichment analyses, although the two species of *Hemiphanes* Förster did not cluster with the other species and were subsequently formally transferred to Cryptinae. In the latter study, Orthocentrinae was most often sister group to Diacritinae and this pairing was sister group to Cylloceriinae.

Given the strong support of Orthocentrinae in other studies, it is likely that the lack of monophyly of Orthocentrinae is artefactual, perhaps because of low taxon sampling and, as discussed by Quicke et al. (2009), relatively high sequence divergence of the 28S D2–D3 region in Orthocentrinae. Addition of more taxa as well as knowledge of larvae including *Proclitus* spp. would help to determine whether Orthocentrinae is monophyletic as well as its relationships within Pimpliformes. In terms of internal relationships within Orthocentrinae, Wahl and Gauld (1998) found that the *Orthocentrus* group was nested within the *Helictes* group as follows: *Aperileptus* Förster + ((*Entypoma* Förster + *Orthocentrus* group) + (all other *Helictes* group genera)). None of our results supported a sister-group relationship of the *Orthocentrus* and *Helictes* groups (i.e., *Orthocentrus* sp. + (*Megastylus* sp. nov. + *Proclitus speciosus*)). When two orthocentrine species clustered together, it was either *Orthocentrus* sp. + *Megastylus* sp. nov. (part 2 of Fig. 117) or *Orthocentrus* sp. + *Proclitus speciosus* (e.g., part 2 of Fig. 118).

Orthopelmatinae

The total-evidence parsimony analysis placed Orthopelmatinae as sister group to all other Ichneumonidae except the exemplars of Xoridinae (part 1 of Fig. 117). In the Bayesian total evidence analysis, Orthopelmatinae was sister group to Xoridinae + (Labeninae + (all exemplars of Ichneumoniformes and Pimpliformes)) (part 2 of Fig. 120).

Previous analyses have had trouble discerning the precise relationships of Orthopelmatinae. Barron (1977) suggested that it was the sister group to Cryptinae, and in turn these two taxa were sister group to Ichneumoninae. Gauld et al. (1997) placed Orthopelmatinae in his Labeniformes, which also included Xoridinae, Labeninae, Agriotypinae, Brachycyrtinae, Cryptinae and Ichneumoninae. Quicke et al. (2000a) using morphological and 28S D2 ribosomal DNA found Orthopelmatinae to be sister group of Ophioniformes, but with no morphological synapomorphies supporting this relationship, and they therefore proposed the informal higher group Orthopelmatiformes for the subfamily. The placement of Orthopelmatinae in Quicke et al. (2009) was unstable as the two combined cladograms placed it with Microleptinae and Oxytorinae either within Ctenopelmatinae (gaps treated as informative) or within Tersilochinae (gaps treated as missing). Quicke et al. (2009) also stated that the sister-group relationship of Orthopelmatinae and Ophioniformes was recovered “with many parameter combinations”. Finally, their analysis with only morphological characters found the

following: (Oxytorinae + (Microleptinae + Orthopelmatinae) + (Neorhacodinae + Tersilochinae))) and this clade was sister group to the remainder of Ophioniformes. In summary, Quicke et al. (2009) suggested that Orthopelmatinae was either sister taxon to Ophioniformes or placed somewhat “basally” within Ophioniformes. Their summary table maintained Orthopelmatinae by itself within Orthopelmatiformes.

None of our analyses recovered a sister-group relationship of Orthopelmatinae and Ophioniformes, although it is noted that moving *O. mediator* as sister to Ophioniformes only lengthened the total-evidence parsimony tree by 9 steps (9926). The parsimony analysis with only morphological characters (part 3 of Fig. 118) found a relationship as follows: *Orthopelma mediator* + (*Phrudus* sp. + (*Allophrys divaricata* Horstmann + (*Stethantyx nearctica* Townes + *Tersilochus* sp.))). It was supported by 15 morphological characters of which 1 was relatively strong: character 28 (state 1): foveate groove of mesopleuron present (C.I. = 0.33) (Fig. 29). This character is one of the important diagnostic characters for Tersilochinae sensu stricto (Tersilochinae of Townes 1971); however it is also present in some of the *Phrudus* group (synonymized with Tersilochinae from Phrudinae by Quicke et al. 2009), as well as sporadically found in other taxa, including *Orthopelma mediator* (but not all species of *Orthopelma*) (Barron 1977). Biologically, Tersilochinae are koinobiont endoparasitoids most often associated with beetles (Khalaim and Broad 2013), but have also been reared from Xyelidae (Hymenoptera) (Khalaim and Blank 2011) and Eriocraniidae (Lepidoptera) (Jordan 1998). Considering the differences between the hosts of Tersilochinae and Orthopelmatinae (endoparasitoids of cynipid gall wasps) (Blair 1945), as well as the fact that the foveate groove is not present in all *Orthopelma* spp., it is likely that the relationship postulated between *O. mediator* and these exemplars of Tersilochinae is artefactual. Similarly, none of our results indicated a close relationship of Orthopelmatinae with Cryptinae or Ichneumoninae as postulated by Barron (1977). The placement of *O. mediator* as sister group to all ichneumonids except the exemplars of Xoridinae (part 1 of Fig. 117) or related to Ichneumoniformes s.l. + Pimpliformes (part 2 of Figs 120, 121) was not expected. In terms of whether to recognize the higher group Orthopelmatiformes, despite ambiguity in its precise relationships, both of our total-evidence analyses found Orthopelmatinae to be sister group to a large number of other subfamilies, therefore maintenance of the higher group Orthopelmatiformes seems valid, at least until such time that more corroborated evidence is found to place Orthopelmatinae more precisely.

Oxytorinae

Our analyses generally placed Oxytorinae (*Oxytorus albopleuralis*) with exemplars of Ophioniformes; however, its placement within this group changed depending on the analysis. In our total-evidence parsimony analysis, Oxytorinae clustered within a clade comprised of all 14 Ctenopelmatinae species as well as Hybrizontinae, Lycorininae, Tatogastrinae, *Chineater masneri* (Mesochorinae) and *Scolomus* sp. (Metopiinae) (part 5 of Fig. 117). See the discussion on Ctenopelmatinae (above) for supporting characters for this clade. In the total-evidence Bayesian analysis, Oxytorinae was placed unresolved in a large clade with exemplars of Ctenopelmatinae, Hybrizontinae, Meso-

chorinae, Metopiinae, Tatogastrinae and the higher Ophioniformes; however, the support for this group was very low (BPP = 53) (part 1 of Fig. 120).

Prior to Townes (1971), *Oxytorus* Förster was considered to be related to genera now classified within Ctenopelmatinae (e.g., within the Mesoleptini of Ashmead 1900). Townes (1971) placed it provisionally in his Microleptinae (questioning whether it belonged there), and Wahl (1990) proposed that it should be placed in its own subfamily because of the lack of characters linking it with other ichneumonid subfamilies. The larva and host are not known, but Wahl (1990) commented that H.K. Townes believed that its notched ovipositor suggested it is probably an endoparasitoid. Gauld et al. (1997) included Oxytorinae in their unplaced subfamilies. Molecular studies have consistently placed Oxytorinae within Ophioniformes. Belshaw and Quicke (2002) using the 28S D2–D3 region and a limited taxon sampling found *Oxytorus* sp. was sister to *Banchus volutatorius* (Linnaeus) (Banchinae) and related to exemplars of Tryphoninae, Lycorininae and Orthopelmatinae. Quicke et al. (2009) generally recovered Oxytorinae within Ophioniformes, related to Banchinae, Ctenopelmatinae, Metopiinae, Neorhacodinae, Stilbopinae, Tersilochinae and Tryphoninae. For example, their combined analysis with gaps treated as missing placed Oxytorinae as sister group to (Tersilochinae + (Microleptinae + Orthopelmatinae)) and more distantly related to Ctenopelmatinae, Tatogastrinae, Mesochorinae and Metopiinae). Our results agree with the placement of *Oxytorus* within Ophioniformes and likely most closely related to Ctenopelmatinae. A more precise placement of Oxytorinae can only be determined by a more comprehensive study of the relationships of Ctenopelmatinae and its relatives.

Pedunculinae

Pedunculinae (*Pedunculus* sp. nov.) was strongly supported as sister group to Claseinae (*Clasis* sp. nov.) in all analyses except the parsimony analysis with only morphological characters in which its relationships were unclear. In both total-evidence analyses, these two subfamilies were placed near the base of Ichneumoniformes s.l. See the sections on Brachycyrtinae, Claseinae and Labeninae (above) for discussion of support of this node and further relationships of Pedunculinae.

Townes (1969) described *Pedunculus*, placing it within Brachycyrtini (Labeninae). Wahl (1993a) raised Brachycyrtini (including *Pedunculus*) to subfamily status. Porter (1998) removed *Pedunculus* to its own subfamily and later, Gauld et al. (2000) included *Adelphion* Townes and *Monganella* Gauld in Pedunculinae. Pedunculinae appear to be supported by presence of a smooth posterior face of the hind tibia (Fig. 69), although this condition has evolved independently in other taxa including *Microleptes* (Microleptinae), some Phygadeuontinae (e.g., *Cisaris* Townes) and some Ctenopelmatinae. Quicke et al. (2009) found that Pedunculinae was sister group to Brachycyrtinae and these two subfamilies were sister group to Claseinae in most of their analyses. As was noted in the discussion of Claseinae, most of our analyses supported a relationship of (*Pedunculus* sp. nov. + *Clasis* sp. nov.) with *Brachycyrtus wardae*, and sometimes these three taxa grouped with Labeninae, but we maintain the subfamily status of all four because of differences in their relationships depending on the characters used and the method of analysis.

Phygadeuontinae

As discussed above in the section on Cryptinae, Phygadeuontinae (*Acrolyta* sp., *Endasys patulus* and *Mastrus* sp.) was supported in both total-evidence analyses (part 3 of Fig. 117, part 2 of Fig. 120), but only moderately so, and was not supported in any other analyses. When supported, it was the sister group of (Alomyinae + Ichneumoninae). The only morphological character supporting this grouping in the total-evidence parsimony analysis was character 53, state 0: fore wing vein *2m-cu* with two bullae (C.I. = 0.07) (Fig. 50) and the Bremer support was only 2 steps, but this sister-group relationship was unequivocally supported in the Bayesian total-evidence analysis (BPP = 100).

Our total-evidence analyses results, albeit with very limited sampling, concur with that of Santos (2017) that Phygadeuontinae (previously Phygadeuontini) is not a tribe within Cryptinae. We did not include specimens of *Hemigaster*, which Santos (2017) moved from Cryptinae (Hemigastrini) to Phygadeuontini, nor did we include specimens of *Helcostizus* Förster which Broad (2016) moved from Phygadeuontini to Cryptini. Whether Phygadeuontinae is monophyletic or needs to be further divided into smaller, natural groups will require future analyses with more taxa. Our analysis certainly concurs with Santos (2017) that Phygadeuontinae is closely related to Cryptinae, Ateleutinae and Ichneumoninae.

Pimplinae

The seven species of Pimplinae (*Perithous divinator*, *Acrotaphus wiltii* (Cresson), *Clistopyga recurva* (Say), *Dolichomitus irritator* (Fabricius), *Zaglyptus pictilis* Townes, *Pimpla annulipes* Brullé and *Theronia bicincta*) never clustered together with unequivocal support in any of our analyses (Table 3); although the total-evidence Bayesian analysis did have moderate support for the monophyly of the subfamily (BPP = 93) (part 2 of Fig. 120). In the total-evidence parsimony analysis, six of the seven species grouped together, the exception being *Pimpla annulipes* (Pimplini), which was part of an unresolved clade including Rhyssinae, Poemeniinae, and the six other species of Pimplinae (part 2 of Fig. 117). Examination of the 1728 equally parsimonious cladograms found that *P. annulipes* was either sister taxon to the rest of the higher Pimpliformes (33% of trees) or sister taxon to Rhyssinae (67% of trees). Moving *P. annulipes* so that it was sister species to the other six species of Pimplinae resulted in an increase in tree length of only three steps (9920). Both analyses using only molecular characters recovered a polyphyletic Pimplinae (part 2 of Figs 119, 121). Finally, the parsimony analysis with only morphological characters recovered the higher Pimpliformes, but the relationships among the Pimplinae species were equivocal (only *Pimpla* and *Theronia* were sister species in all trees) (part 1 of Fig. 118). Examination of the individual equally parsimonious trees found that Pimplinae was monophyletic in 87 % of the 3872 trees, as opposed to 13% that had *D. irritator* as sister taxon to Rhyssinae, the latter topology supported by characters associated with parasitism of wood-boring hosts, e.g., character 96(2): ovipositor longer than length of metasoma and character 140(1): oviposition through lignified tissue.

Historically, Pimplinae in the broad sense (i.e., including related taxa such as Poemeniinae and Rhyssinae) was one of the five traditional subfamilies of Ichneumonidae

(Holmgren 1857). The morphology-based classification of Townes (1969) used a tribal classification within Pimplinae (his “Ephialtinae”) to attempt to define natural groups. Some of these tribes were later raised to subfamily status (e.g., Diacritinae, Poemeniinae, Rhyssinae) (Eggleton 1989, Gauld 1991). More recent morphological phylogenetic studies analyzed the relationships within Pimplinae (Wahl and Gauld 1998, Gauld et al. 2002b). Both of these studies provided strong support for the monophyly of Pimplinae. In contrast, recent molecular studies have found varied levels of support for Pimplinae. Belshaw et al. (1998) using a limited taxon sampling of Pimplinae never recovered the subfamily as monophyletic. The study of Quicke et al. (2009) does not explicitly comment on the monophyly of Pimplinae in their analyses with only molecular characters, but they do present data on the monophyly of Pimplini with differing gap extension and opening costs, and the majority of these molecular analyses did not recover Pimplini as monophyletic. Finally, the study of Klopstein et al. (2019) had varied results. Their transcriptome analysis with five species of Pimplinae using amino acids recovered Pimplinae, but the similar analysis with nucleotides did not. In addition, none of their hybrid enrichment analyses recovered Pimplinae because *Xanthopimpla varimaculata* Cameron never clustered with all of the other 24 pimpline exemplars. Their three hybrid enrichment analyses with amino acids did recover the other 24 exemplars as monophyletic but the two analyses with nucleotides did not. Klopstein et al. (2019) speculated that the placement of *Xanthopimpla* in their analyses may be because of a long branch of their exemplar species, or it may indicate an actual relationship requiring formal recognition of a new tribe or subfamily. In terms of formal changes in Pimplinae, Klopstein et al. (2019) resurrected Theroniini, comprised of the *Theronia* group of genera, which did not generally cluster with Pimplini. In summary, most previous morphological analyses have supported Pimplinae, although the current analysis is equivocal. In contrast, most molecular analyses have not found strong support for Pimplinae, regardless of the genes used or the method of analysis.

With respect to the placement of Pimplinae in the current study, when there was some support for the family (in 87% of the trees in the morphology-only parsimony analysis and the Bayesian total-evidence analysis with BPP = 93), Pimplinae was sister to (Poemeniinae + Rhyssinae). This is the same as the relationship postulated by the morphological analysis of Wahl and Gauld (1998), the combined morphology and molecular analysis of Quicke et al. (2009) and all analyses using amino acids in Klopstein et al. (2019).

Concerning tribal monophyly and their relationships, the following previous hypotheses have been postulated:

- 1) (Delomeristini (not including *Perithous* Holmgren) + (Ephialtini + (*Perithous* + Pimplini including the *Theronia* group))) (morphological parsimony analysis of Wahl and Gauld 1998);
- 2) (Pimplini + (Delomeristini including *Perithous*) + Ephialtini)) (morphological parsimony analysis of Gauld et al. 2002b);
- 3) (Delomeristini (including *Perithous*) + (Pimplini + Ephialtini)) (combined morphological and molecular parsimony analysis of Quicke et al. 2009);

- 4) (Delomeristini (including *Perithous* and *Pseudorhyssa*) + Theroniini) + (Pimplini + Ephialtini), with *Xanthopimpla* clustering outside Pimplinae) (anchored enrichment analysis using amino acids of Klopstein et al. 2019).

The current study supported monophyly of Ephialtini in all studies except parsimony with only morphological data. For example, the Bayesian total-evidence analysis had the following topology: (*Perithous divinator* + *Theronia bicincta*) + (*Pimpla annulipes* + (*Dolichomitus irritans* + (*Acrotaphus wiltii*/ *Clistopyga recurval* *Zaglyptus pictilis*))). (part 2 of Fig. 120). The latter four species comprise Ephialtini and the support for this tribe was unequivocal (BPP = 100). The total-evidence parsimony analysis was similar but more resolved: (*D. irritator* + (*Z. pictilis* + (*A. wiltii* + *C. recurva*))) with 13 synapomorphies and a Bremer support of 5 steps (part 2 of Fig. 117). Relative to the four previous hypotheses of relationships listed above, the current Bayesian total evidence analysis supported the relationships of Klopstein et al. (2019) in that *Theronia bicincta* (Theroniini) was sister to *Perithous divinator* (Delomeristini), not sister to *Pimpla annulipes* (Pimplini).

Poemeniinae

Poemeniinae (*Neoxorides caryae* (Harrington) and *Poemenia albipes*) was supported unequivocally in all analyses except the Bayesian analysis using only molecular characters (Table 3), and even the latter analysis still had moderate support with a posterior probability of 94 (part 2 of Fig. 121). The subfamily was supported by 26 synapomorphies (9 morphological) in the total-evidence parsimony analysis with a Bremer support of 5 steps (part 2 of Fig. 117). One of the morphological characters was uniquely derived: character 15(1): foramen magnum laterally expanded.

In terms of relationships, there was strong support for Poemeniinae being the sister group to Rhyssinae (e.g., Bayesian total-evidence, BPP = 99) (part 2 of Fig. 120). The parsimony total-evidence analysis did not contradict this grouping, although the strict consensus was unresolved in this part of the tree with the following clade with equivocal relationships: Poemeniinae/ *Pimpla annulipes*/ Rhyssinae/ other Pimplinae (part 2 of Fig. 117). Thirty-three percent of the shortest trees recovered Poemeniinae + Rhyssinae. Furthermore, most analyses placed Poemeniinae within the higher Pimpliformes (e.g., Bayesian total-evidence had a posterior probability of 98 for this grouping). See discussion of Pimpliformes (above) for support of this grouping in the parsimony total-evidence analysis.

Historically, *Poemenia* Holmgren was placed within the traditional "Pimplinae" of early authors, e.g., Holmgren (1860). Townes (1969) considered *Poemenia* and relatives as a tribe within Ephialtinae (= Pimplinae), and it was only with the study of Gauld (1991) based on the thesis of Eggleton (1989) that the group was raised to subfamily status. Wahl and Gauld (1998) confirmed the subfamily status within Pimpliformes with a phylogenetic analysis of morphological characters that found the following relationship: Pimplinae + (Rhyssinae + Poemeniinae). They also defined three tribes: Pseudorhyssini comprised of *Pseudorhyssa*, Rodrigamini comprised of *Rodrigama* Gauld and Poemeniini comprised of all other genera. The current study was only

able to include species of Poemeniini. Quicke et al. (2009) included exemplars of all three tribes. Their morphological analysis hypothesized that *Pseudorhyssa* belonged to Pimplinae, not Poemeniinae, a placement that was previously suggested (e.g., Townes 1969). In contrast, the combined morphology and sequence analyses of Quicke et al. (2009) had equivocal placement for *Pseudorhyssa*, including related to Pimplinae, Rhyssinae, or Poemeniinae, as sister to (Rodrigamini + Poemeniini). They left *Pseudorhyssa* as unplaced in their summary table.

More recently, *Pseudorhyssa* clustered within Pimplinae in all of the full-data-set analyses of Klopstein et al. (2019) which led them to formally move the genus back to Pimplinae. Since the current analysis did not include *Pseudorhyssa* or *Rodrigama*, we cannot comment on these taxa, but we can state that there was strong support for the monophyly of Poemeniini and for the relationship of Poemeniini (at least) to Rhyssinae.

Rhyssinae

Similar to Poemeniinae, Rhyssinae (*Megarhyssa greenei* Viereck, *Rhyssa crevieri* (Provancher) and *Rhyssella nitida* (Cresson)) was well-supported – it was unequivocally monophyletic in all of our analyses (Table 3). In the total-evidence parsimony analysis, Rhyssinae was supported by 56 synapomorphies including 13 morphological, of which two were uniquely derived: character 92, state 1: apical segment of female metasoma elongate with a horn or boss (Fig. 82); and character 93 state 1: posterior sternites of female metasoma with tuberculate ovipositor guides (Fig. 84). The Bremer support was greater than 10 steps. Rhyssinae is likely the most well-supported subfamily within Ichneumonidae. All of our analyses placed Rhyssinae within the higher Pimpliformes (with Poemeniinae and Pimplinae) and when there was resolution within this group, the sister group for Rhyssinae was Poemeniinae (e.g., part 1 of Fig. 120).

As described above for Poemeniinae, *Rhyssa* Gravenhorst and its relatives were also historically placed in the traditional Pimplinae (Holmgren 1860) (= equals our higher Pimpliformes). Phylogenetic studies have confirmed this placement (Wahl and Gauld 1998; Quicke et al. 2009, Klopstein et al. 2019, and most analyses in the current study). Based on the strength of evidence supporting the higher Pimpliformes, it could be argued that a reversion to a previous concept of Pimplinae is warranted (including poemeniines and rhyssines). Considering that the limits of Poemeniinae were just changed by the removal of *Pseudorhyssa* and the fact that we were not able to include *Rodrigama* in our analysis, we believe this move would be premature. Maintenance of these taxa in three subfamilies is more prudent until additional studies are able to confirm the current definitions and relationships of all groups within higher Pimpliformes.

Sisyrostolinae

Sisyrostolinae (*Brachyscleroma* sp. and *Erythrodoilius calamitosus* Seyrig) was not recovered as monophyletic in any of our analyses (Table 3). Having said this, these two species often clustered in close proximity to each other along with exemplars of Tersilochinae. For example, in the total-evidence parsimony analysis, all five tersilochine species, together with the two sisyrostoline species formed a clade that was supported

by 20 synapomorphies (of which 4 were morphological), with a Bremer support of 2 (part 4 of Fig. 117). Two of these characters had a relatively high consistency index: character 109, state 1: larval mandible conical and with small, apical tooth (CI = 0.80) (Fig. 111), and character 139, state 3: Coleoptera host (CI = 0.27). Similarly, these seven species clustered together in the total-evidence Bayesian analysis, but with a low support value (BPP = 78) (part 1 of Fig. 120). The larvae of both *Brachyscleroma* Cushman and *Erythrodoilius* Seyrig are unknown, as is the host of *Erythrodoilius*.

The genera to which our two exemplars of Sisyrostolinae belong were, until recently, included in the subfamily Phrudinae (e.g., Townes 1971; Gauld et al. 1997). The relatedness of Tersilochinae and Phrudinae was implied by their placement next to each other in Townes (1971). The latter author did; however, express doubt regarding the monophyly of Phrudinae, and Gupta (1994) in his revision of *Brachyscleroma* stated “The Phrudinae contains a heterogenous assemblage of genera which are certainly not related.” Conversely, Gauld et al. (1997) stated with respect to the small, temperate genera (i.e., the *Phrudus* group of genera) and the large, mostly Afrotropical *Erythrodoilius* group of genera that they were “correctly associated” with each other. The latter study cited “the peculiarly narrow proboscis fossa” as an autapomorphy of Phrudinae.

More recent phylogenetic studies investigated the monophyly of Phrudinae. Quicke et al. (2009) included 12 phrudine exemplars. In all their analyses, three *Erythrodoilius* species clustered with their other two members of the *Erythrodoilius* group (*Melanodolius* sp. and *Icariomimus* sp.) and the sister taxon of this group was *Brachyscleroma* sp. The relationship of this clade to the *Phrudus* group; however, was equivocal. In their combined analysis with gaps treated as missing, the *Phrudus* group was monophyletic and clustered with Tersilochinae, whereas (*Brachyscleroma* sp. + the *Erythrodoilius* group) was placed separate to Tersilochinae (near Tryphoninae). In contrast, in their combined analysis with gaps treated as informative, exemplars of two genera of the *Phrudus* group (*Phrudus* Förster and *Astrenis* Förster) were sister group to *Brachyscleroma* sp. + the *Erythrodoilius* group). Whereas these are only two of many analyses that Quicke et al. (2009) performed, it illustrates the fact that there may (or may not) be a relationship between the *Erythrodoilius* group + *Brachyscleroma* and at least some of the *Phrudus* group. Despite this ambiguity, Quicke et al. (2009) formally divided the Phrudinae of Townes (1971), placing all of the *Phrudus* group within Tersilochinae and resurrecting Brachyscleromatinae Townes to accommodate *Brachyscleroma* and the *Erythrodoilius* group as well as the Oriental and Eastern Palaearctic *Lygurus* Kasparyan. Since that time, Sheng and Sun (2011) described another genus in this group: *Laxiarella* Sheng & Sun from the Oriental region. Bennett et al. (2013) noted the priority of the name Sisyrostolinae for this higher group. Quicke et al. (2009) provided a diagnosis for Sisyrostolinae as follows: 1) sternites mostly sclerotized and laterotergites large; 2) scape cylindrical (rather long and narrow); 3) proboscis fossa strongly narrowed; 4) ovipositor lacking notch; 5) hind wing vein *M* + *Cu* long relative to vein *1-M*.

Our analyses do not uphold the monophyly of Sisyrostolinae, nor its separate status from Tersilochinae (including the *Phrudus* group). It is likely that the *Erythrodoilius* group is monophyletic (*Melanodolius* Saussure and *Icariomimus* Seyrig are very closely

related based on morphology, for example, the frons in all three genera bears a longitudinal ridge, and the latter may even be paraphyletic with respect to *Erythrodoilius* (Bennett et al. 2013). Whether the *Erythrodoilius* group is only distantly related to Tersilochinae or nested within Tersilochinae is unclear at present. The sister-group relationship of *Brachyscleroma* to the *Erythrodoilius* group was not upheld by this study, and this needs to be re-examined. Similarly, the relationship of the *Phrudus* group to Sisyrstolinae needs to be studied (see Tersilochinae, below). This statement is based on the fact that all of our analyses and some of Quicke et al. (2009) did not recover a monophyletic *Phrudus* group, as well as the fact that some taxa putatively placed within the *Phrudus* group have never been assessed cladistically (e.g., *Notophrudus* Porter). Similarly, *Lygurus* and *Laxiareola* have not been sequenced or coded for morphology to examine where they fit. Finally, with respect to the five diagnostic characters that Quicke et al. (2009) used to define Sisyrstolinae, none of them are convincing autapomorphies of the group because all of them also occur in members of the *Phrudus* group, for example, most *Astrenis* spp. have much more sclerotized sternites than any member of Sisyrstolinae. It should be noted that despite careful examination of many specimens of the *Erythrodoilius* group, the *Phrudus* group and the Tersilochinae sensu stricto, we were unable to code the proboscival fossa character of Gauld et al. (1997). Because of the large amount of work still remaining to be done on this part of the tree, we refrain from making any formal changes at this time. We do, however, concur with Townes (1971) and Quicke et al. (2009) that Sisyrstolinae belongs to Ophioniformes, not Pimpliformes (= the traditional Pimplinae) as Seyrig (1932) proposed. Our study placed them within Ophioniformes, but not within the higher Ophioniformes which is in accordance with the findings of Quicke et al. (2009).

Stilbopinae

The two species of Stilbopinae (*Stibops vetulus* and *Notostilbops* sp. nov.) were never sister taxa in any of our analyses (Table 3). *Notostilbops* sp. nov. clustered with the four species of Banchinae in all analyses except the parsimony analysis with only morphological characters and consequently we have formally moved *Notostilbops* to Banchinae. See Banchinae section (above) for justification of this taxonomic change.

Tatogastrinae

Tatogastrinae (*Tatogastra nigra*) was one of the small subfamilies that clustered within the “Ctenopelmatinae and related subfamilies” clade in the total-evidence parsimony analysis (part 5 of Fig. 117). It was placed in a clade that lacked internal resolution as follows: Oxytorinae/ Tatogastrinae/ (*Chineater masneri* + *Scolomus* sp.) based on 39 synapomorphies (six of which were morphological) and a Bremer support of 2 steps. It occupied a similar position in the Bayesian total-evidence analysis (part 1 of Fig. 120), as sister species to (*Chineater masneri* + *Scolomus* sp.) in a very poorly supported group (posterior probability = 55). See the discussion on Ctenopelmatinae (above) for additional discussion of the relationships of *Tatogaster* to Ctenopelmatinae, Metopiinae and Hybrizontinae in the Bayesian total evidence analysis.

In terms of previous hypotheses concerning the relationships of Tatogastrinae, Wahl (1991) performed a morphological phylogenetic analysis and proposed that Tatogastrinae was the sister group of Ophioninae on the basis of four synapomorphies: 1) fore wing with spurious vein originating at distal end of vein 1A; 2) glymma of T1 absent and T1 enveloping S1; 3) profile of propodeum not angulate; and 4) ovipositor short, about equal in length to the depth of the metasoma. The current analysis did not code the spurious vein. It is present in *Tatogaster* and in our five ophionine species including *Hellwigia obscura*, but apparently absent in *Hellwigia elegans* Gravenhorst. The vein also appears to be present in some taxa outside of Ophioninae, especially in larger-bodied species (e.g., *Metopius pollinctorius*, *Megarhyssa greenei*, *Netelia* sp.), and therefore it may be related to species size as much as phylogeny. The current analysis coded the fusion of T1 and S1 (character 81) for *Tatogaster* as state 1: fused, but suture visible, compared to Ophioninae as state 2: fused, suture not visible (i.e., character coded somewhat differently than in Wahl 1991). In terms of profile of the propodeum (character 35), the current analysis coded about two thirds of the exemplar taxa as state 1: rounded to flattened without separate dorsal and posterior faces and the consistency index of this character is very low (0.03) with multiple parallelisms and reversals which makes it difficult to determine its apomorphic state. Ovipositor length (character 96) has a similarly low consistency index (0.05). Moving *Tatogaster nigra* as sister group to Ophioninae increased the tree length to 9955 (+ 38 steps).

The morphological analysis of Quicke et al. (2009) and their combined morphology and 28S D2–D3 analysis found Tatogastrinae to be the sister group to Mesochorinae with both of these subfamilies related to various tribes of Ctenopelmatinae. In terms of morphology, the similarly large, rhombic areolet of Tatogastrinae and Mesochorinae was noted as a possible synapomorphy of these two taxa although several differences were also noted (presence of a dorsal notch in the ovipositor of Tatogastrinae, lack of a glymma, and lack of rod-like gonoforceps). Moving *T. nigra* as sister group to Mesochorinae (except for *Chineater masneri*) in our analysis increased the tree length to 9941 (+ 24 steps). In summary, the current analysis found no evidence supporting a sister-group relationship to Ophioninae or Mesochorinae (except the enigmatic genus *Chineater*), but it did suggest a relationship of Tatogastrinae with our exemplars of Ctenopelmatinae, albeit with weak support.

Tersilochinae

As discussed in Sisyrostolinae (above), the five species of Tersilochinae sensu lato (*Allophrys divaricata*, *Phrudus* sp., *Peucobius fulvus* Townes, *Stethantyx nearctica* and *Tersilochus* sp.) did not cluster together in any analyses, except in a grouping that also included the two species of Sisyrostolinae (in both total-evidence analyses) (Table 3). See the section on Sisyrostolinae for a discussion of the support for this grouping.

In contrast, the Tersilochinae sensu stricto, which is equivalent to the Tersilochinae of Townes (1971), is a well-supported group in all analyses (Table 3). For example, in the total-evidence parsimony analysis, this clade – *Stethantyx nearctica* + (*Allophrys divaricata* + *Tersilochus* sp.) was supported by 63 characters, 18 of which were mor-

phological, and a Bremer support of more than 10 steps. Despite the fact that none of the morphological synapomorphies were uniquely derived, several had a relatively high consistency index, for example, character 4, state 1: clypeal margin with uniform fringe of setae (C.I. = 0.25) (similar to Fig. 12); character 16, state 1: maxillary palpus four-segmented (C.I. = 0.33); and character 64, state 1: basal 0.6 of hind wing vein *M* + *Cu* spectral (C.I. = 0.33) (Fig. 58).

Our study generally supports a relatively close relationship of the *Phrudus* group and Tersilochinae sensu stricto; however, *Erythrodolius* and *Brachyscleroma* (Sisyrostolinae) clustered within this clade as follows: (*Phrudus* sp. + (*Erythrodolius calamitosus* + *Peucobius fulvus*)) + (*Brachyscleroma* sp. + Tersilochinae sensu stricto) (e.g., part 4 of Fig. 117, part 1 of Fig. 120). More work is needed to determine whether Tersilochinae sensu lato needs to be broadened to include some or all of the genera currently placed in Sisyrostolinae. Paramount in these studies is increased knowledge of the larva in this clade. The current study reports the first larval description of the *Phrudus* group of genera (Appendix 1) including a putative synapomorphy for the *Phrudus* group and Tersilochinae sensu stricto: character 109, state 1: larval mandible cone-shaped with small, apical tooth (C.I. = 0.8) (Fig. 111). Examination of the larva of other *Phrudus* group specimens and Sisyrostolinae would be very helpful to determine the relationships within this clade. Another character that requires additional examination in the *Phrudus* group, Tersilochinae sensu stricto and Sisyrostolinae are the modified sensory structures of the sub-basal flagellomeres reported by Vikberg and Koponen (2000), which were not coded in the current study. In our exemplar species, they are present in *Phrudus* sp., *Stethantyx nearctica* and *Tersilochus* sp. and possibly in *Allophrys divaricata* (hard to score because of setae and small size), but apparently absent from *Brachyscleroma* sp., *Erythrodolius calamitosus*, and *Peucobius fulvus*. Finally, our results agree with Broad (2016), that Neorhacodinae is not a synonym of Tersilochinae as Quicke et al. (2009) proposed, but should be treated as a separate subfamily (see Neorhacodinae, above).

Tryphoninae

Tryphoninae (*Eclytus* sp., *Idiogramma longicauda*, *Zagryphus nasutus* (Cresson), *Netelia* sp., *Phytodietus vulgaris*, *Cteniscus* sp., *Cycasis rubiginosa* (Gravenhorst) and *Polyblastus* sp.) was not supported in any of our analyses (Table 3); however, the total-evidence parsimony analysis did find that all eight tryphonine species shared a common ancestor, but also including *Neorhacodes enslini* (Neorhacodinae) (part 4 of Fig. 117). This grouping was supported by 24 synapomorphies, of which 7 were morphological, including one uniquely derived: character 136, state 1: egg exits body ventral to ovipositor and stalk travels down lumen of ovipositor. The Bremer support was 6 steps. Note that egg morphology and method of oviposition are unknown for *N. enslini* (and were therefore coded as “?”). The parsimony analysis using only morphology did not support any groupings within Tryphoninae, except for Phytodietini (*Phytodietus vulgaris* + *Netelia* sp.) (part 2 of Fig. 118). The other three analyses all placed the tryphonine exemplars near the base of the tree, often in a grade. For example, the total-evidence Bayesian analysis had *Neorhacodes enslini* as sister to all other Ichneumonidae, followed

by Phytodietini and then a clade of equivocal relationships comprised of *Lycorina glaucomatal* *Idiogramma longicaudal* (*Zagryphus nasutus* + (*Eclytus* sp. + (*Polyblastus* sp. + (*Cteniscus* sp. + *Cycasis rubiginosa*)))) (part 1 of Fig. 120).

Historically, Tryphoninae was one of the five major groups of Ichneumonidae (Holmgren 1857), but this included many taxa that were later removed to their own subfamilies (e.g., Ctenopelmatinae, Metopiinae, etc.) by Townes et al. (1961) and later authors. Townes et al. (1961) presumably based the definition of Tryphoninae sensu stricto on possession of stalked eggs, a trait recognized as an important indicator of phylogeny as early as Hartig (1837). Short (1978), studying the larva of *Euceros* spp. (Eucerotinae), confirmed the conclusions of Perkins (1959a) that Eucerotinae (which also has a stalked egg) does not belong to Tryphoninae. Later, Shaw (2004) and Coronado-Rivera et al. (2004) described the stalked egg of *Lycorina* spp. (Lycorininae), which raised the possibility that *Lycorina* should be moved to Tryphoninae. See the Lycorininae section (above) for the reasons against this move.

In terms of phylogenetic analyses, Belshaw et al. (1998) using the 28S D2 region found that *Netelia* sp. was paraphyletic with respect to the other five tryphonine exemplars. The later, more comprehensive, combined morphological and molecular analysis of Quicke et al. (2009) found that all of their 62 tryphonine species shared a common ancestor, but species of Sisyrastolinae, Stilbopinae, Eucerotinae and *Ischyrocnemis* (Metopiinae) were also nested in this clade. Bennett (2015) using only morphological characters and a limited number of outgroups, did recover Tryphoninae as monophyletic with three uniquely derived synapomorphies: the clypeal fringe of setae, the larval mandible lacking denticles on the dorsal surface of the blade and stalked eggs.

Based on the current study, Quicke et al. (2009) and Bennett (2015), there is some evidence for the monophyly of Tryphoninae; however, more knowledge is needed about taxa that may be related (or may belong) to Tryphoninae (e.g., Neorhacodinae, Lycorininae, Sisyrastolinae, Stilbopinae). Knowledge of whether the body of the egg travels down the lumen of the ovipositor in these taxa could alter their placement relative to Tryphoninae, as occurred previously for the genus *Acaenitellus* Morley (see Gupta 1988). In addition, an increase in our knowledge of Tryphoninae larval characters and hosts would also help clarify whether Tryphoninae is monophyletic (host order is only known for 29 of the 54 extant genera) (Bennett 2015). With respect to *Neorhacodes*, the known host of *N. enslini* (*Spilomena* spp.) (Hymenoptera: Crabronidae) was coded the same (character 139, state 1) as most tribes of Tryphoninae which parasitize sawflies. Perhaps coding this character differently for Aculeata as opposed to sawflies would be appropriate and would modify the placement of *Neorhacodes* relative to Tryphoninae.

With respect to the findings of Belshaw et al. (1998) that Phytodietini may be related to, but not included within Tryphoninae, the current study is equivocal. Both Bayesian analyses and the parsimony analysis with only morphological characters found that Phytodietini did not cluster with the other six exemplars of Tryphoninae, but the total-evidence parsimony analysis did. In order to accept the notion that Phytodietini do not belong to Tryphoninae, one has to postulate that evolution of the stalk

of the egg travelling down the lumen of the ovipositor during oviposition has evolved twice. A future study including the morphological characters of Bennett (2015) and sequence data obtained by next generation sequencing will address this issue.

Relationships within Tryphoninae based on the total-evidence parsimony analysis were as follows: (Neorhacodinae + Phytodietini) + (Idiogrammatini + (*Polyblastus* group of Tryphonini + (Eclytini + Oedemopsini) + *Exenterus* group of Tryphonini))) (part 4 of Fig. 117). Ignoring the placement of Neorhacodinae, the relationships differ from the morphological cladistic analysis of Bennett (2015) in two ways: 1) Phytodietini is the sister group to the rest of Tryphoninae (Idiogrammatini was the sister group in the latter study); 2) Tryphonini (including the *Exenterus* group) is not monophyletic (the *Exenterus* group of genera clustered within Tryphonini in the latter study). It is difficult to draw conclusions on relationships within Tryphoninae from the current analysis because of the low sample size (only 8 of 54 extant genera in five of seven tribes). Future studies will include a greater number of taxa including exemplars of Sphinctini and Ankylophonini.

Xoridinae

Xoridinae (*Aplomerus* sp., *Odontocolon albotibiale* (Bradley) and *Xorides stigmapterus* (Say)) was recovered as monophyletic in the parsimony analysis using only morphological characters, as well as both Bayesian analyses. In the morphological parsimony analysis (part 1 of Fig. 118), lack of resolution near the base of the tree precludes any statements about its placement within Ichneumonidae, except that it does not belong in the higher Ophioniformes. In both Bayesian analyses, Xoridinae was related to Ichneumoniformes and Pimpliformes, not Ophioniformes. The total-evidence Bayesian analysis placed Xoridinae within the Ichneumoniformes/ Pimpliformes grouping as follows: Orthopelmatinae + (Xoridinae + (Labeninae + (remainder of Ichneumoniformes s.l. + Pimpliformes))) (part 2 of Fig. 120). The Bayesian analysis with only molecular characters had a similar topology as follows: (Orthopelmatinae + Xoridinae) + (Labeninae + (Ichneumoniformes s.l. except Labeninae + Pimpliformes)) (part 2 of Fig. 121). In contrast, the total-evidence parsimony analysis found that *Aplomerus* sp. was sister taxon to all other Ichneumonidae as follows: *Aplomerus* sp. + ((*Odontocolon albotibiale* + *Xorides stigmapterus*) + (*Orthopelma mediator* + all other Ichneumonidae)) (part 1 of Fig. 117).

With respect to the monophyly of Xoridinae, on the basis of morphology alone, Xoridinae is well-supported, with 23 synapomorphies, including one uniquely derived: character 113, state 1: larval mandible with spines at base of blade (part 1 of Fig. 118). A previous morphological cladistic analysis supports this assertion (Gauld et al. 1997). Similarly, the combined morphological and molecular analysis of Quicke et al. (2009) recovered Xoridinae as monophyletic when treating gaps as missing or informative, although the latter analysis included specimens of *Xorides*, *Odontocolon* and *Ischnoceros* Gravenhorst, but not *Aplomerus*, which Gauld et al. (1997) found to be the sister group to the other three genera. Quicke et al. (2009) also coded morphology at the subfamily level for Xoridinae, and some of their analyses with only molecular data did not support the monophyly of the subfamily. In summary, based

on morphological evidence and the majority of our results, is it likely that Xoridinae is monophyletic. The lack of monophyly of Xoridinae in our total-evidence parsimony analysis was possibly because of how the parsimony algorithm dealt with the sequence data (as evidenced by the fact that Xoridinae was monophyletic in the Bayesian total-evidence analysis). Note that the larva of *Aplomerus* is unknown, and if it is confirmed that *Aplomerus* larvae also bear spines at the base of their mandible, this would help confirm the monophyly of the subfamily.

In terms of the placement of Xoridinae within Ichneumonidae, the total-evidence parsimony analysis provides some support that Xoridinae (or a subset of xoridine taxa) is the sister group of all other Ichneumonidae. Quicke et al. (1999) using only 28S DNA sequence data for 24 ichneumonoids and two aculeate outgroups found that *Xorides praecatorius* (Fabricius) was sister species to all other ichneumonoids. Similarly, the transcriptome analysis of Klopstein et al. (2019) with six braconid outgroups and their anchored enrichment analyses with six braconids and three non-ichneumonoids also had *X. praecatorius* as sister to all other ichneumonoids. Therefore there is evidence that Xoridinae is sister-group to all other Ichneumonidae, but the results of our Bayesian analyses refute this, and therefore, future analyses involving only ichneumonid taxa should investigate the effects of different rootings on ingroup topology, rather than only root their trees with Xoridinae. In terms of the recognition of the higher group Xoridiformes, because both of our total-evidence analyses found that Xoridinae is the sister group to a large number of other subfamilies, this seems valid at this point.

Biological transitions

Inclusion of biological characters in our data matrix allows an examination of the evolution of these characters within Ichneumonidae, at least with respect to the exemplar taxa used in this analysis. In terms of the validity of this kind of analysis, we agree that biological characters can be complex and our unweighted, unordered analysis may not take into account differences in the likelihood of particular character state changes evolving relative to others. Despite this, we believe that there is value in this kind of analysis. An unweighted, unordered analysis is objective. It does not place pre-conceived notions on the direction of evolution, nor does it make subjective decisions on the relative importance of characters. Whether the current analyses of the evolution of biological characters in Ichneumonidae is realistic or over-simplistic is a question that will hopefully foster discussion on the evolution of these interesting traits, producing hypotheses that can be tested by future analyses.

Three biological characters have been optimized on to the total-evidence parsimony strict consensus cladogram as follows: character 137: timing of larval maturation (Fig. 122); character 138: location of larval maturation (Fig. 123); and character 139: host order/ source of larval nutrition (Fig. 124). In addition to optimization on these characters on the parsimony tree, a comparison is made of differences and similarities of the evolution of each character hypothesized by the total-evidence Bayesian analysis (Fig. 120).

Timing of larval maturation

In the total-evidence parsimony analysis, character 137, timing of larval maturation, had a length of 8 steps (Fig. 122). The following transitions occurred: koinobiosis to idiobiosis (five times): 1) *Doryctes erythromelas* (Braconidae); 2) at base of (*Odontocolon albotibiale* + *Xorides stigmapterus*); 3) at base of higher Pimpliformes; 4) at base of Ichneumoniformes s.l.; 5) *Cratichneumon w-album* (Cresson); idiobiosis to koinobiosis (three times): 1) *Acrotaphus wiltii*; 2) *Euceros* sp. nov.; 3) Ichneumoninae including *Alomya debellator*. Optimization of the character using ACCTRAN or DELTRAN did not change the number and placement of transitions.

The ancestral state for Ichneumonidae favours koinobiosis, although this requires some discussion. The state is unknown for *Aplomerus* sp. (Xoridinae) and is equivocal for the next node (the other two xoridines which are both idiobionts). There is strong morphological evidence that *Aplomerus* Provancher belongs to Xoridinae (Gauld et al. 1997) and therefore, it is likely to be an idiobiont. If this is true, then the ancestral state for Ichneumonidae would be idiobiosis for timing of larval maturation. Additional taxa, for example, a species of *Ischnoceros* Gravenhorst (Xoridinae) should be included to re-evaluate this question, and hopefully also additional knowledge of biology of our exemplar species.

In terms of the direction of evolution of this character in the parsimony analysis, it has transitions in both directions, slightly favoured in the direction of koinobiosis to idiobiosis (five times) compared to vice versa (three times). The transition from a supposedly more specialized koinobiont to a less specialized strategy (idiobiosis) was not hypothesized by Gauld (1988a). Considering the size and age of Ichneumonidae (at least 85 mya) (Kopylov 2012), it is, perhaps, not surprising that transitions appear to have arisen in both directions in this character over the course of evolution of the family. Estimates of the age at which parasitism first evolved within Hymenoptera, i.e., the age of the taxon *Vespina* (= Orussoidea + Apocrita) is at least 164 mya (Rasnitsyn and Zhang 2004; Ronquist et al. 2012). Based on these ages, there is no reason to assume that the koinobiont life history strategy had not evolved prior to the origin of Ichneumonoidea. In terms of a mechanism to explain transitions from koinobiosis to idiobiosis, this simply requires a change in the timing at which the larva commences feeding and/or a change in the host-searching behaviour of the female wasp. It has been argued that delay in the commencement of larval feeding should be advantageous to the parasitoid because it provides a larger host on which to feed and takes advantage of host behaviours such as finding a secure location for pupation away from predators and parasitoids (Gauld 1988a). It could be argued; however, that when there are high populations of parasitoids and predators that specialize on finding large, exposed, wandering larvae, reverting to an idiobiont strategy on younger larvae could be favourable in order to avoid this pressure. In addition, the evolution from late larval-pupal koinobionts to pupal-pupal idiobionts could easily evolve by the female wasp delaying and modifying its host-searching behaviour in order to search for pupae rather than late larvae/ pre-pupae. Whereas pupae are generally more concealed than larvae and therefore harder to find, they lack the ability to defend themselves physically and are generally

less setose/ spinose, so if they can be found, they may be easier to parasitize successfully. This type of transition appears to have evolved at least once in Ichneumonidae in our parsimony analysis in *Cratichneumon w-album* (green to red transition in Fig. 122).

Comparing the evolution of this character in the total-evidence Bayesian analysis, koinobiosis is favoured as plesiomorphic within Ichneumonidae (Fig. 120). The state of the sister taxon of all other Ichneumonidae (*Neorhacodes enslini*) is not known, but Phytodietini (sister taxon to all Ichneumonidae except *Neorhacodes*) are koinobionts, as are related taxa. The length of the character in the Bayesian analysis is 7 steps. Three transitions from koinobiosis to idiobiosis (indicated by the letter “I” in Fig. 120) occur as follows: 1) the outgroup *Doryctes erythromelas*; 2) *Cratichneumon w-album*; and 3) the ancestor of (Xoridinae + (Labeninae + (Ichneumoniformes s.l. + Pimpliformes))). Four changes occur from idiobiosis to koinobiosis: 1) *Euceros* sp.; 2) *Acrotaphus wiltii*; 3) the ancestor of Ichneumoninae (including *Alomya debellator*) and the ancestor of Acaenitinae, Orthocentrinae, Diplazontinae and related subfamilies (shown in Fig. 120 with a “K”). In summary, regardless of the method of phylogenetic analysis, transitions have occurred in both directions with respect to timing of larval maturation, and perhaps unexpectedly, koinobiosis appears more likely to be the plesiomorphic state within Ichneumonidae.

Location of larval maturation

Examination of the evolution of ectoparasitism versus endoparasitism (character 138) in the total-evidence parsimony analysis reveals that ectoparasitism is plesiomorphic in both Braconidae and Ichneumonidae (Fig. 123). As discussed for timing of larval maturation (above), our limited outgroups affected the plesiomorphic state for Braconidae (in this case with two ectoparasitoids versus one endoparasitoid) which in concert with the state for (*Odontocolon albotibiale* + *Xorides stigmapterus*) made the state at the base of Ichneumonidae unequivocally ectoparasitoidism. The length of the character is 12 steps. Unlike in character 137, the evolution of this character differed based on the type of character optimization used. Under ACCTRAN, transitions from ectoparasitism to endoparasitism occurred eight times: 1) *Aleiodes terminalis* (Braconidae); 2) ancestor of all Ichneumonidae except Xoridinae; 3) *Pimpla annulipes*; 4) *Theronia bicincta*; 5) *Euceros* sp. nov. 6) *Microleptes* sp.; 7) Ichneumoninae including *Alomya debellator*; 8) *Neorhacodes enslini*. Transitions from endoparasitism to ectoparasitism occurred three times: 1) ancestor of higher Pimpliformes; 2) ancestor of Ichneumoniformes s.l.; 3) ancestor of Tryphoninae (including *Neorhacodes enslini*). In addition, within Ophioniformes, Lycorinae (*Lycorina glaucomata*) had a transition from endoparasitism (state 1) to endoparasitism with a final ectoparasitoid phase followed by pupation within the host cocoon (Shaw 2004) (state 2, not shown in Fig. 123).

In contrast, under DELTRAN optimization (not shown), transitions from ectoparasitism to endoparasitism occurred ten times: 1) *Aleiodes terminalis* (Braconidae);

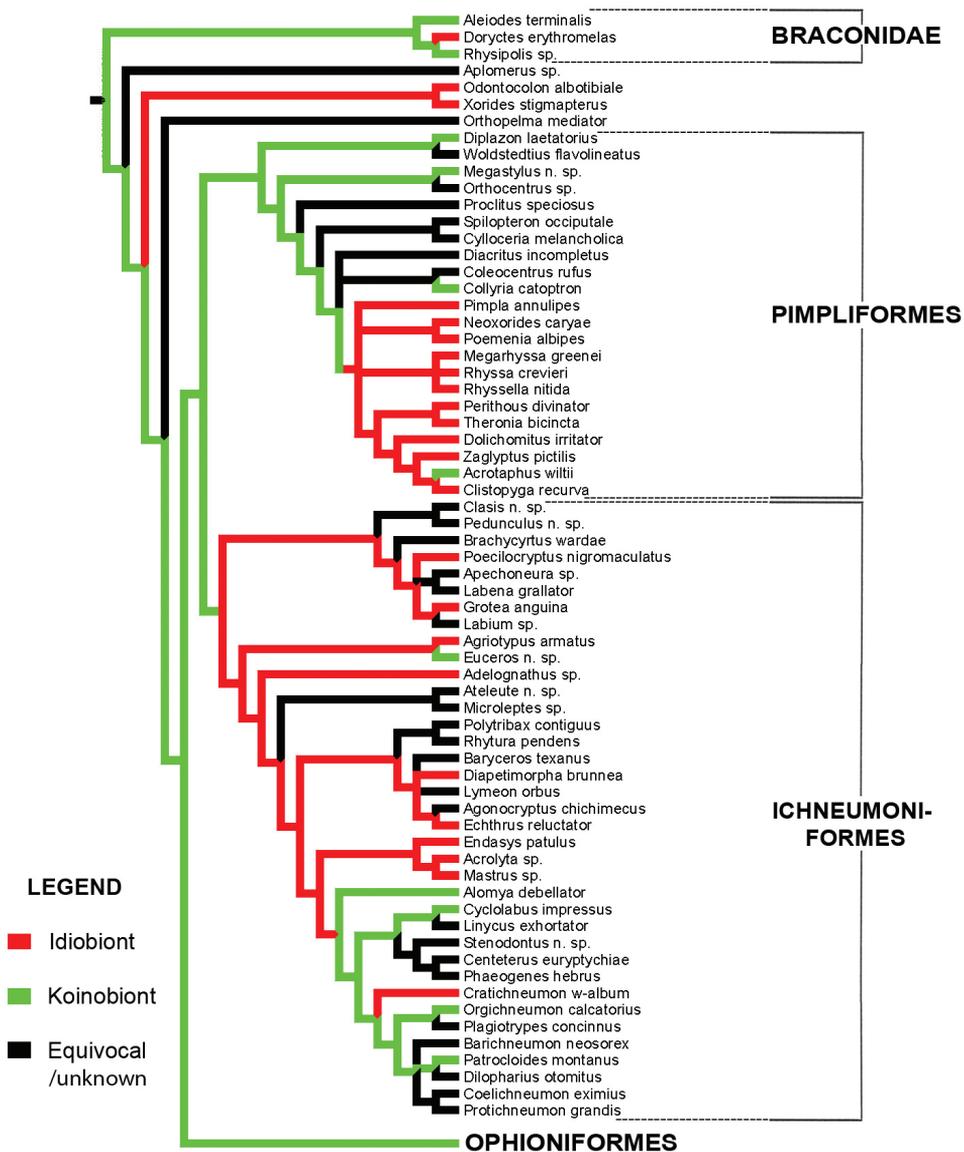


Figure 122. Optimization of character 137 (timing of larval maturation) on total-evidence parsimony analysis strict consensus cladogram using ACCTRAN. See Legend for description of colour coding for character states. Character length = 8 steps.

2) Orthopelmatinae; 3) ancestor of Pimpliformes; 4) *Pimpla annulipes*; 5) *Theronia bicincta*; 6) *Euceros* sp. nov. 7) *Microleptes* sp.; 8) Ichneumoninae including *Alomya debellator*; 9) *Neorhacodes enslini*; 10) ancestor of Ophioniformes. Only one transition from endoparasitism to ectoparasitism occurred in the ancestor of higher Pimpliformes. Lycorininae had the same transition to state 2 as for ACCTRAN.

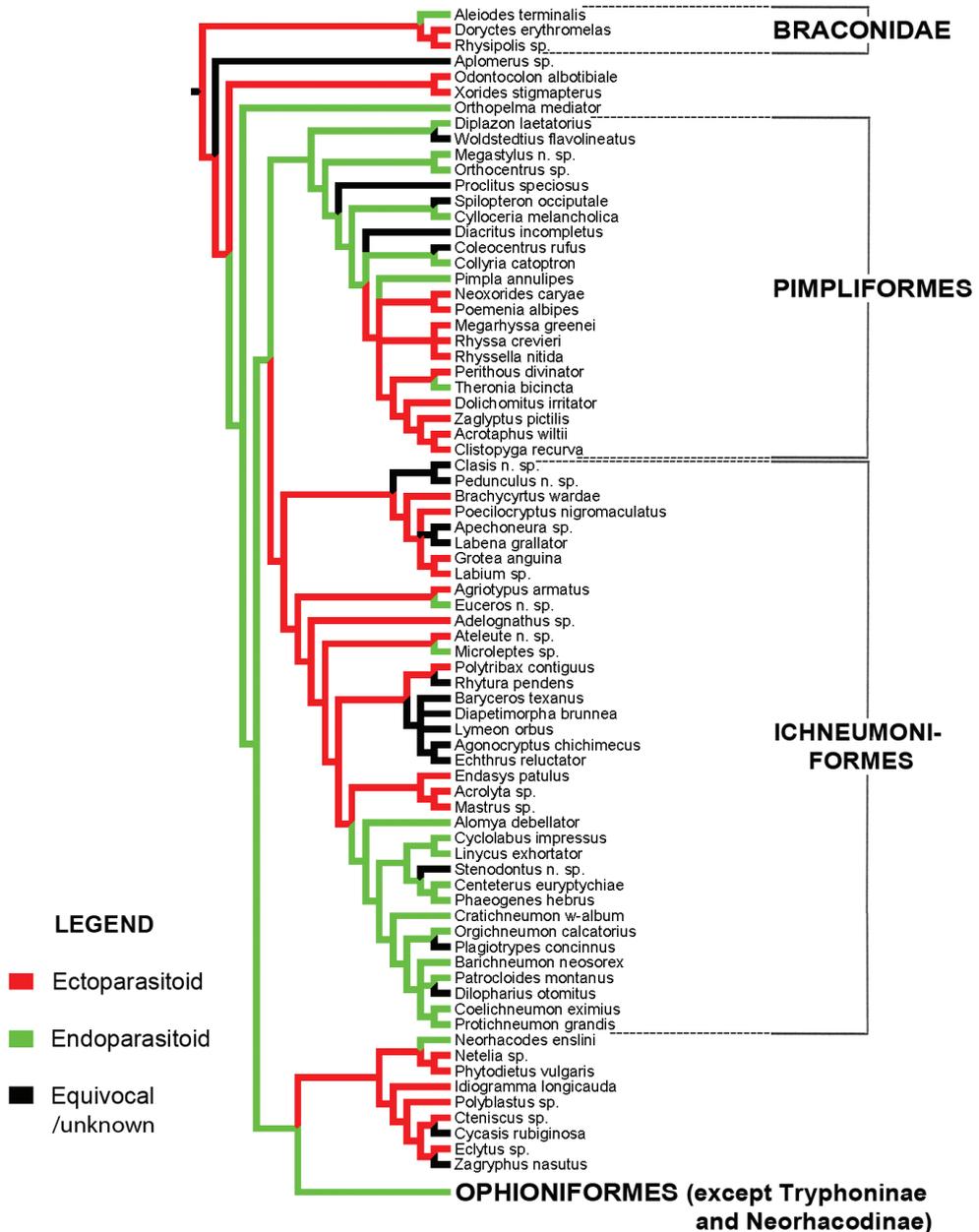


Figure 123. Optimization of character 138 (location of larval development) optimized on total-evidence parsimony analysis strict consensus cladogram using ACCTRAN. See Legend for description of colour coding for character states. Character length = 12 steps.

Gauld (1988a) provided several hypotheses regarding the evolution of endoparasitism, all of which postulated that it evolved from ectoparasitism. These hypotheses are mostly supported by the transitions observed in the total-evidence parsimony analysis.

Gauld (1988a) did not discuss the possibility that ectoparasitism could evolve via a reversal from an endoparasitoid state, although the results of Sharanowski et al. (2011) did question the hypothesis that ectoparasitism was plesiomorphic in Braconidae. Intuitively, the transition from endoparasitism to ectoparasitism appears more difficult to explain than a reversal from koinobiosis to idiobiosis. Evolution of endoparasitism can involve changes to the method of oviposition by the female wasp (Boring et al. 2009) and structure of the ovipositor (Belshaw et al. 2003; Quicke et al. 2000b), but also changes in the ovaries and egg morphology (Iwata 1960), venom properties (Moreau and Asgari 2015) and in some groups, co-evolution with polydnnaviruses that alter host development via endocrinological changes (Tanaka and Vinson 1991; Pennacchio and Strand 2015), not to mention, major changes in larval wasp morphology (Short 1978; Wahl 1986, 1988, 1990). It is hard to imagine that any parasitoid lineage would be able to revert back to ectoparasitism following evolution of all the specialized attributes of an endoparasitoid lifestyle, although intuitively, some of the traits listed above may be just as easy or easier to lose, than to gain (e.g., association with polydnnaviruses). Regardless, according to the parsimony total-evidence analysis, transitions from endoparasitism to ectoparasitism appears to have occurred at least once (DELTRAN optimization) or three times under ACCTAN optimization. In comparison, the total-evidence Bayesian analysis contradicts the total-evidence parsimony analysis with respect to the topology of Pimpliformes. In the Bayesian analysis, the ectoparasitoid higher Pimpliformes is sister group to the remaining endoparasitoid subfamilies (Acaenitinae, Orthocentrinae, Diplazontinae, etc.), therefore there is no transition from endoparasitism to ectoparasitism in the Pimpliformes. That is not to say that the Bayesian analysis unequivocally supports the hypothesis that endoparasitism evolves from ectoparasitism and never the reverse. In Fig. 120, this character has 11 steps, of which there are nine transitions from ectoparasitism to endoparasitism (nodes or taxa indicated by “EN”) and one transition from endoparasitism to ectoparasitism in the node that supports Xoridinae + (Labeninae + (all remaining Ichneumoniformes + Pimpliformes))) (indicated by “EC”). In addition, there is one change from ectoparasitism to the state in Lycorininae (indicated by “E2”). In summary, ectoparasitism is plesiomorphic within Ichneumonidae, regardless of the analysis. The transition from ectoparasitism to endoparasitism is far more common than the reverse, but there is at least one transition from endoparasitism to ectoparasitism hypothesized in both of our total-evidence analyses, despite the fact that the mechanism by which this transition could evolve is not easily explained intuitively.

Host/ source of larval nutrition

The order of host/ source of larval nutrition used by our exemplar taxa (character 139) is optimized on the total-evidence parsimony strict consensus tree in Fig. 124 using ACCTAN. The length of the character is 28 steps and the ancestral state for Ichneumonidae is parasitism of Hymenoptera. Under DELTRAN optimization (not

shown), the ancestral state for Ichneumonidae is Lepidoptera. However, if the host of *Aplomerus* (Xoridinae) is coded as Coleoptera rather than unknown, based on its morphological similarity to known Xoridinae which are beetle parasitoids, the state at the base of Ichneumonidae changes to Coleoptera for the total-evidence parsimony analysis, regardless of the type of optimization. Finally, the Bayesian total-evidence analysis hypothesizes that Lepidoptera parasitism is plesiomorphic for Ichneumonidae (Fig. 120, character optimization not shown). Even though the sister group of all other Ichneumonidae (*Neorhacodes enslini*: Neorhacodinae) is a parasitoid of aculeate wasps (Hymenoptera), the next two “basal” taxa in the Bayesian analysis parasitize Lepidoptera (Lycorininae and Phytodietini (Tryphoninae)) as do two of the three outgroups (*Aleiodes terminalis* and *Rhysipolis* sp.).

In terms of additional evidence supporting one of these three host orders as plesiomorphic for Ichneumonidae, all easily pre-date the origin of Ichneumonidae (at least 85 mya) (Kopylov 2012). Based on the fossil record, Coleoptera is the oldest of the three, first appearing in the Permian (290 mya) (Kukalová-Peck and Beutel 2012) and it was highly speciose and well-diversified by the upper Cretaceous (Smith and Marcot 2015). Hymenoptera is of similar age, with estimates that the order began to diversify 281 mya (Peters et al. 2017). In contrast, the oldest known Lepidoptera fossil is lower Jurassic (190 mya) (Whalley 1985). Therefore based on the fossil record, it has been assumed that Lepidoptera is the youngest of the insect orders and diversified with the radiation of angiosperms (Wahlberg et al. 2013), although the relatively recent origin and diversification has been questioned because of poor preservation of Lepidoptera relative to other orders (Sohn et al. 2015). Regardless, hosts of all three orders were present at the origin of Ichneumonidae, therefore any could have been the ancestral host order for Ichneumonidae.

A comparison of the relative frequencies of host use of the four major holometabolous orders in our parsimony analysis shows that Lepidoptera is the most prevalent host (for 35 % of our 131 exemplar ichneumonid species), compared to Hymenoptera (30 %), Coleoptera (12 %) and Diptera (5 %). These percentages are comparable to the known host use by ichneumonids at the subfamily level: Lepidoptera (18 subfamilies, 43 % of total); Hymenoptera (16 subfamilies, 38 %); Coleoptera (13 subfamilies, 31 %) and Diptera (8 subfamilies, 19%) (Wahl 1993c; Yu et al. 2016; Bennett, unpublished).

Examination of the different transitions that occur within this character in the parsimony total-evidence tree reveals that of the 28 state changes, there were 13 different types of transitions, (e.g., Lepidoptera to Coleoptera, Hymenoptera to Coleoptera, etc). The order that was most often plesiomorphic in the state changes was Hymenoptera with the following apomorphic states and number of changes: changes to Lepidoptera (8); Coleoptera (5); Diptera (1); Neuroptera (1); Trichoptera (1) and facultatively herbivorous (1). The next most common order that was plesiomorphic in these transitions was Lepidoptera, as follows: changes to Coleoptera (4); Hymenoptera (2) and Diptera (1). Thirdly, there were two transitions from Diptera: one to Coleoptera and one to Hymenoptera. Lastly, there was one transition from Coleoptera to egg predation and one change from egg predation to parasitization of spiders. Therefore,

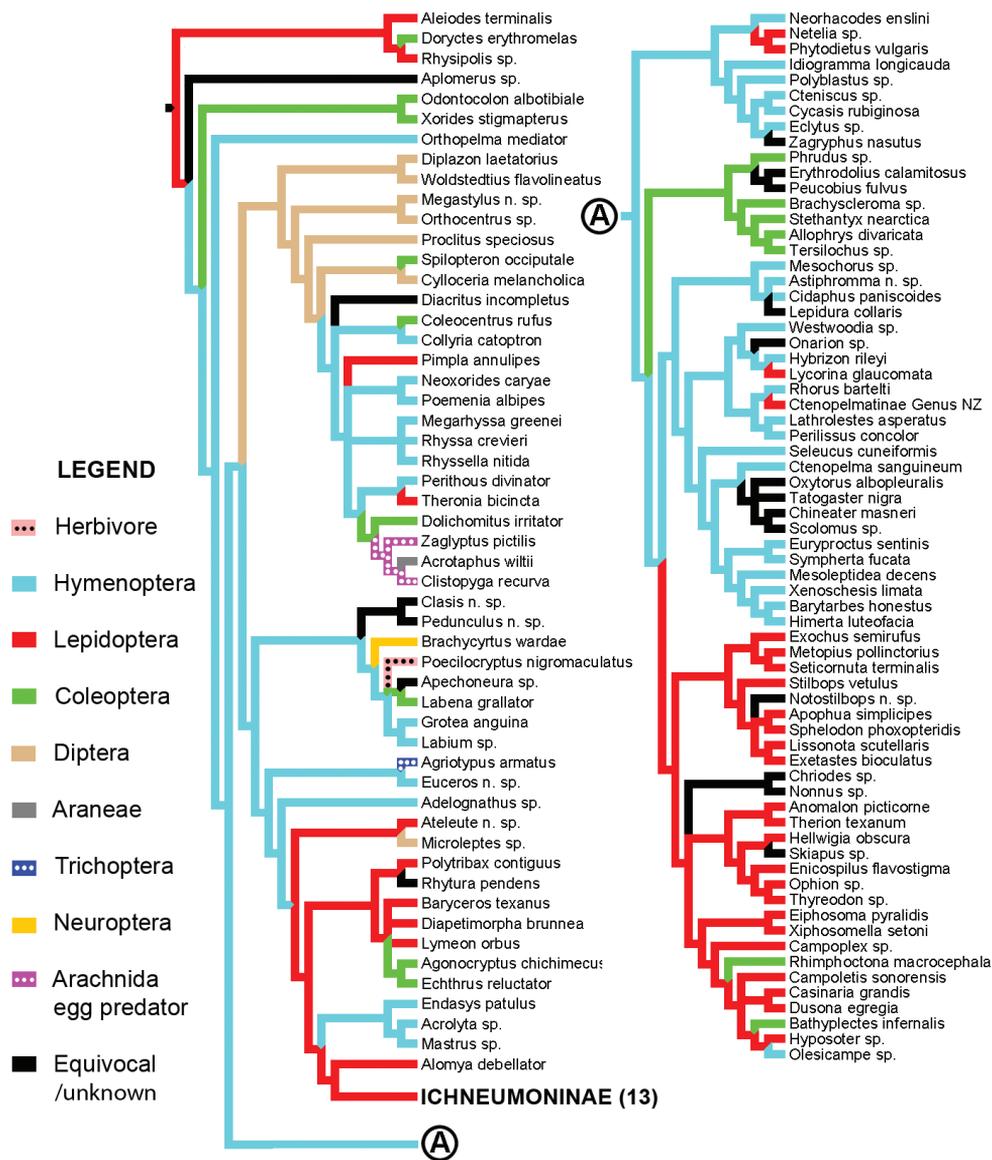


Figure 124. Optimization of character 139 (host) optimized on total-evidence parsimony analysis strict consensus cladogram using ACCTRAN. See Legend for description of colour coding for character states. Character length = 28 steps.

ichneumonids that parasitize Hymenoptera appear much more likely to switch to different host orders compared to, for example, an ichneumonid that parasitizes Lepidoptera, Diptera or Coleoptera. In fact, over half of all of the total host transitions (17 of 28 state changes) in Fig. 124 have Hymenoptera as the plesiomorphic state. This implies that when an ichneumonid group parasitizes Hymenoptera, it may somehow be better adapted to host-switch to another order; or stating this another way, there may be impediments to host switching when an ichneumonid evolves to parasitize, for

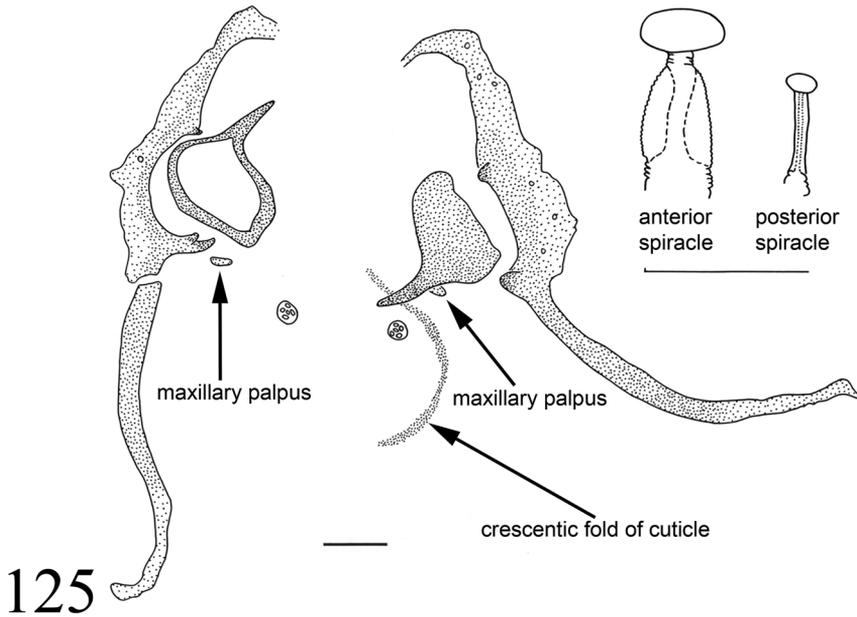


Figure 125. *Alomya semiflava* Stephens. Cephalic sclerites and spiracles of mature larva. Australian National Insect Collection. Scale bars: 0.1 mm. Structures are drawn as seen on slide (not duplicated bisymmetrically) because of distortion of the sclerites.

example, Diptera or Coleoptera. It is not clear what characters may be associated with the ability/ inability to switch hosts. Of course, this analysis is on a very broad scale and a more in-depth analysis including more species may reveal a different pattern.

Conclusions

Overall, the two total evidence analyses obtained the most resolution of relationships, followed by the molecular analyses and finally, the parsimony analysis with only morphological and biological characters. There was general congruence between the parsimony and Bayesian total-evidence analyses, except for at the base of Ichneumonidae (described below).

The relative support of different groupings within Ichneumonidae is shown in Table 3. Of the three major subfamily groupings, Pimpliformes was most well-supported (four of five analyses). A large portion of Ichneumoniformes s.l. (i.e., the group comprised of Cryptinae, Ichneumoninae, Phygadeuontinae, Ateleutinae, Adelognathinae and Microleptinae) was supported in both total evidence analyses, although the relationship to other subfamilies that have previously been placed in Ichneumoniformes (e.g., Agriotypinae) was equivocal, depending on the analysis. The Ophioniformes was only supported in the total-evidence parsimony analysis, whereas in the Bayesian total evidence analysis it formed a grade at the base of Ichneumonidae. With respect to internal arrangements within the three major groupings, the core of Ichneumoniformes

s.l. (listed above) was the most consistently recovered across analyses, whereas many of the relationships within Ophioniformes and especially, within Pimpliformes differed between the parsimony and Bayesian analyses. The ambiguity of relationships within Pimpliformes in the current study mirrored those of Klopstein et al. (2019).

In both total evidence analyses, Pimpliformes was sister group to Ichneumoniformes s.l., which agrees with Santos (2017) and Klopstein et al. (2019), but disagrees with Quicke et al. (2009) which supported Pimpliformes + (Ophioniformes + Ichneumoniformes s.l.). The sister group of all other Ichneumonidae was equivocal depending on the analysis. Xoridinae was only sister group in the total-evidence parsimony analysis and was not monophyletic in this analysis. Labeninae was related to / included in Ichneumoniformes s.l., not sister group to all other Ichneumonidae or sister to all ichneumonids except Xoridinae.

There were several other well-supported groupings of subfamilies including higher Pimpliformes, higher Ophioniformes, (Claseinae + Pedunculinae) and (*Stilbops* + Banchinae including *Notostilbops*). At the subfamily level, some subfamilies were well-supported across analyses: Banchinae (including *Notostilbops*), Campopleginae, Cremastinae, Diplazontinae, Ichneumoninae (including *Alomya*), Labeninae, Mesochorinae (excluding *Chineater*), Metopiinae (excluding *Scolomus*), Poemeniinae, Rhyssinae and Tersilochinae s.s. Moderate support (i.e., support in two to three analyses) was found for Anomaloninae, Cryptinae, Ophioninae, Phygadeuontinae and Xoridinae. Weak support (i.e., in only one analysis) was found for Acaenitinae, Nesomesochorinae and Orthocentrinae.

In contrast, the following subfamilies were never supported: Ctenopelmatinae, Pimplinae, Sisyrostolinae, Stilbopinae, Tersilochinae s.l. and Tryphoninae. Ctenopelmatinae was supported in the total-evidence parsimony analysis with the inclusion of Hybrizontinae, Lycorininae, Oxytorinae and Tatogastrinae. Tryphoninae was also supported in this analysis with the inclusion of Neorhacodinae. The most equivocally-placed subfamilies were Lycorininae, Neorhacodinae, Orthopelmatinae and Xoridinae.

Optimization of biological characters on the total evidence phylogenies hypothesized that for Ichneumonidae, ectoparasitism is plesiomorphic to endoparasitism. The ancestral state for timing of larval maturation is koinobiosis in both analyses; however, the lack of data for the sister taxon to all other ichneumonids in the parsimony analysis (*Aplomerus*) raises some doubt regarding this hypothesis. If *Aplomerus* is an idiobiont (as expected), then the parsimony analysis would support idiobiosis as plesiomorphic to koinobiosis. Finally, the ancestral host for Ichneumonidae is hypothesized to be Hymenoptera or Lepidoptera, although if the host of *Aplomerus* is determined to be Coleoptera (as expected), then Coleoptera would be the hypothesized ancestral host in one of the five analyses.

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Appendix I

Taxonomic descriptions

Cephalic sclerites of mature larva of *Phrudus defectus* Stelfox.

Fig. 111

Cephalic sclerites mostly well-sclerotized. Epistomal suture (character 105): region distorted and not reconstructed in drawing, but possibly completely sclerotized and forming epistomal band (coded as “?”). Labral sclerite (character 108) & clypeolabral plates (character 130) unknown because labral region distorted (both scored as “?”). Stipital sclerite present, more or less horizontal and median end contacting labial sclerite (character 119, state 0) and without lateral plate-like extension (character 120, state 0). Pleurostoma only partially visible due to distortion; posterior struts of inferior mandibular processes not connected by band (character 114, state 0); inferior mandibular process dorsad to dorsal margin of labial sclerite (character 107, state 0); accessory pleurostomal area (character 106) not discernible (coded as “?”). Hypostoma well-sclerotized and long (character 115, state 0); lateral end simple, not divided or upcurved (character 116, state 0). Hypostomal spur present and long, about 2.0× as long as its basal width (character 117, state 0), meeting stipital sclerite near middle (character 118, state 0). Labial sclerite nearly circular (character 124, state 1), about as long as wide (character 125, state 0), not produced ventrally as a spine (character 126, state 0). Salivary orifice U-shaped (character 133, state 1). Prelabial sclerite absent (character 127, state 0). Sclerotized plate ventrad labial sclerite absent (character 129, state 0). Maxillary and labial palpi each bearing 2 sensilla (character 123, state 0). Mandible uniformly well-sclerotized (character 111, state 0), cone-shaped and apex with small, tooth-like projection (character 109, state 1) (Fig. 111, upper left); blade without denticles (character 112, state 2), without accessory teeth (character 110, state 0) and without basal spines (character 113, state 0). Antenna (character 131): unknown (coded as “?”). Spiracle with closing apparatus separated by section of trachea (character 132, state 0 - coded as “?” in matrix). Skin with numerous small triangular projections (10 μ long) and scattered elongate setae (32 μ long).

Material examined: *Phrudus defectus* Stelfox last larval instar exuvium slides: UNITED KINGDOM: Isle of Man, Laxey, Baldhoon Road, Crofton, SC4284; F.D. Bennett; from *Epuraea melanocephala* in sycamore flowers; exposed 1–2.vi.2008, adult emerged 4.v.2009 [DBW preparation 28.I.2012b] (EMUS); UNITED KINGDOM: Isle of Man, Laxey, Mooar Glen, SC43284; F.D. Bennett; from *Epuraea melanocephala* in sycamore flowers; collected 31.v.2008, adult emerged 11.v.2009 [DBW preparation 28.I.2012c] (EMUS).

Comments. Distortions of the two preparations (DBW preparations 28.I.2012b and 28.I.2012c) do not allow clear views of the dorsal portion of the cephalic capsule, and hence structures above the inferior mandibular processes are not shown. Figure 111 is a composite of the two preparations listed above. This is the first description of the larva of the *Phrudus* group of Tersilochinae which is of interest because prior to

Quicke et al. (2009), the *Phrudus* group was part of its own subfamily (Phrudinae). The shape of the mandible (apex with small, tooth-like projection) (character 109, state 1) is a synapomorphy for the *Tersilochus* and *Phrudus* groups of genera, thereby supporting the inclusion of these two groups in Tersilochinae.

Cephalic sclerites of mature larva of *Collyria* spp.

Fig. 112

Cephalic sclerites mostly weakly sclerotized or absent. Epistomal suture unsclerotized (character 105, state 0). Labral sclerite absent (character 108, state 1). Clypeolabral plates absent (character 130, state 0). Stipital sclerite absent (character 119, state 2) and without lateral plate-like extension (character 120, state 0). Pleurostoma difficult to discern, but apparently not laterally expanded (character 106, state 0) and posterior struts of inferior mandibular processes short and not obviously connected by band (character 114, state 0). Hypostoma absent (character 115, state 2). Hypostomal spur absent (character 117, state 2). Labial sclerite (character 124) difficult to discern ventrally, therefore shape scored as “?”. Salivary orifice (character 133) not visible (scored as “?”). Prelabial sclerite absent (character 127, state 0). Sclerotized plate ventrad labial sclerite absent (character 129, state 0). Maxillary and labial palpi (character 123) not visible (scored as “?”). Mandible (scored for *C. coxator* from the description of Salt 1931): uniformly sclerotized (character 111, state 0) and triangular (character 109, state 0); blade without denticles (character 112, state 2), accessory teeth absent (character 110, state 0), basal spines absent (character 113, state 0). Mandible apparently absent in *C. catoptron* (Fig. 112). Antenna absent (character 131, state 2). Spiracle with closing apparatus separated by section of trachea (character 132, state 0). Skin with numerous small bubble-like projections and lacking setae.

Material examined: *Collyria coxator* (Villers) last larval instar exuvium slide mount: Locality unspecified. Label 1: Slide no. 284. Don G. Salt. Label 2: *Collyria calcitrator* (Grav.) JRTS 1955 (NMNH); *Collyria catoptron* Wahl slit and macerated last instar whole larva slide mount: CHINA, Gansu Province, Yuzhong County, ix.1998, ex. *Cephus fumipennis*, T. Shanower et al. [DBW preparation 3.I.2011] (EMUS).

Comments: The nature of the cephalic sclerites of the mature larva of *Collyria* is not straightforward. Salt (1931) gave a detailed description of the larval stages of *Collyria coxator* (Villers). The mature larval head was characterized as “not at all darkened or hardened, is without any noticeable facial rods, and appears to lack even mandibles.” He went on to state: “Careful staining, however, shows that the mandibles and some of the usual facial rods are represented, but not well developed... The mandibular struts may be clearly distinguished, and there are vague sclerotic areas in the labral region, but all parts are so poorly represented that it is difficult to homologize them”. Salt’s drawing (his fig. 13b), shows only the pleurostomae and mandibles (the mandibles drawn with a finer line), all other cephalic sclerites being absent (the large square structure below the mandibles is the suspensorium of the hypopharynx, as pointed out by Short

(1959)). Short (1959) illustrated another specimen of *C. coxator* and gave a detailed description of it. Examination of the original slide (NMNH) reveals part of the drawing to be imaginary: only the pleurostomae and suspensorium of the hypopharynx are present, and the mandibles and antennae are absent. The mandibles in the drawing may have been added to conform to Salt's figure.

Between Salt's detailed study and Short's slide, *Collyria* appears to be quite unique amongst the Ichneumonidae for the drastic reduction of the cephalic sclerites. Reduction of the sclerites is associated with not spinning a cocoon (such as in the Anomaloninae, Ichneumoninae, Metopiinae, and Pimplini), but never to such an extent as in *Collyria*. Preserved larvae of a second species, *Collyria catoptron* Wahl, were available for comparison. A number of larvae were longitudinally slit and macerated in sodium hydroxide solution, with the resulting skins stained with acid fuchsin and then slide mounted. Whole larvae were also stained with acid fuchsin and then examined. No evidence of sclerotized structures could be found on the mounted skins. The stained whole specimens showed the general mouthpart regions as convexities and furrows but no sclerotized structures were present (Fig. 112).

In summary, *Collyria* lacks all cephalic sclerites except for the pleurostoma, part of the labium and maxilla and the mandibles (at least in *C. coxator*). It might be noted that Short depicted the spiracle's closing apparatus as extremely long and narrow. The spiracles in Short's slide and the new specimens of *catoptron* are not nearly as long or as narrow (his depiction of the closing apparatus being separated from the atrium is accurate). Short apparently did not use a camera lucida or ocular grid, and his drawings are often strikingly distorted.

Cephalic sclerites of mature larva of *Alomya semiflava* Stephens

Fig. 125

The following description is based on a re-examination of two larval slides prepared by J.R.T. Short (Hinze and Short 1983). Our figure of the last instar larva is depicted as it appears on the slide (i.e., not reconstructed as bilaterally symmetrical, as per usual practice) because the larva on the slide is distorted. In addition, the suspensorium of the hypopharynx is not shown, as its presence is universal within ichneumonids and its shape uninformative. See comments below for additional description of Short's slide preparation and how it was depicted in Hinze and Short (1983).

Cephalic sclerites with many prominent structures absent; remaining structures well-sclerotized. Epistomal suture completely sclerotized, uncertain if forming epistomal band because of distortion of larva, but coded as present (character 105, state 2). Labral sclerite absent (character 108, state 1); clypeolabral plates absent (character 130, state 0). Stipital sclerite absent (character 119, state 2). Pleurostoma well-sclerotized, not laterally expanded (character 106, state 0); posterior struts of inferior mandibular processes short and not connected by band (character 114, state 0). Hypostoma long and well-sclerotized (character 115, state 0), more or less straight, markedly angled ventrally towards cephalic

midline. Hypostomal spur absent (character 117, state 2). Labial sclerite absent (character 124), originally coded as present, (circular to ovoid: state 1), but re-assessed when manuscript in press" (see comments, below). Region near salivary orifice distorted, but presumably U-shaped (character 133, state 1). Prelabial sclerite absent (character 127, state 0). Plate ventrad labial sclerite absent (character 129, state 0). Maxillary and labial palpi each bearing 5 sensilla (character 123, state 2). Mandible large, uniformly well-sclerotized (character 111, state 0) and triangular (character 109, state 0); blade without denticles (character 112, state 2). Antenna (character 131) not visible (coded as "?"). Spiracle with closing apparatus adjacent to atrium (character 132, state 1, but coded as separated from atrium, state 0). Skin smooth with scattered short setae.

Material examined: 1 last larval instar slide mount, larva reared under laboratory conditions from mummified final larval instar of *Korscheltellus* (= *Hepialus*) *lupulinus* (Linnaeus, 1758), 1979, R. Hinz (ANIC). 1 penultimate stage larval slide mount. Same data as final instar (ANIC).

Comments: *Alomya semiflava*, like other species in its genus, attack species of *Hepialidae* (Lepidoptera) (Waterston 1926, Hinz and Short 1983). The wasp is a koinobiont endoparasitoid, with the unusual habit of pupating within the hardened remains of the host larva in contrast to most other ichneumonines which pupate within the host pupa (*Colpognathus* spp. are also known to pupate in the host larval remains – see Shaw and Bennett 2001). Short characterized both of his slide preparations as ‘final larval instars’, but one is clearly penultimate stage. Points of interest are as follows:

- 1) There is no trace of the antennal disc.
- 2) The region of the epistomal suture is distorted, and it is not possible to determine if an epistomal band is present (it could be there but thin and not well sclerotized). The band is present in the penultimate larva slide, but ichneumonid larvae often lose structures upon maturity (Wahl 1990).
- 3) Short reported cuticular folds bearing setae on the clypeolabrum but these could not be seen. He apparently thought these to be analogous to the narrow clypeolabral plates found in *Phaeogenini*.
- 4) The maxillary apices are distorted and could not be reconstructed as depicted by Short. Both maxillary palpi are rotated so that only lateral views were possible (Fig. 125) (and so the five sensilla in Short's figure were a reconstruction, albeit probably correct). Wrinkles in the cuticle led Short to depict the presence of stipital sclerites; they are not present.
- 5) The region of the salivary orifice is distorted and its shape cannot be determined (although it is presumably U-shaped). What Short depicts as the ‘silk press’ is the terminal end of the salivary duct.
- 6) Short shows the labial sclerite to be present, with the ventral section unsclerotized. The actual specimen has a crescentic structure on the right side in the vicinity of the labium (Fig. 125, crescentic fold of cuticle) but there is not a corresponding structure on the left side. Given the general distortion of the specimen, the crescentic structure is interpreted as an extended cuticular wrinkle.

- 7) The orientation of the epistoma+pleurostoma+hypostoma is difficult to determine, given the preparation's distortion. The left-side hypostoma has broken off from the pleurostoma. The slide of the penultimate instar has the orientation of Short's figure but the right side of the mature larval specimen belies that reconstruction. The actual arrangement is probably similar to that of *Thyrateles procax* (Cresson) or *Trogus pennator* (Fabricius) in Gillespie and Finlayson (1983).

In summary, the cephalic morphology of the final-instar larva of *A. semiflava* is that of a standard ichneumonine, lacking only clypeolabral plates.

Appendix 2

Taxa sequenced, countries of collection, specimen voucher numbers and Genbank accession numbers for molecular vouchers. All sequences were original to this study except as noted by superscripts indicating literature reference: ¹Heraty et al. (2011); ²Quicke et al. (2006); ³Quicke et al. (2009); ⁴Belshaw and Quicke (2002); Taxonomy reflects nomenclature prior to current study.

Taxa	Country of collection	Voucher depository	Voucher number	Genbank accession numbers		
				COI	28s D2	EF1a
Braconidae						
<i>Doryctes erythromelas</i> (Brullé)	?	UKY	?	GQ374627 ¹	GQ374709 ¹	GQ410706 ¹
<i>Rhyssipolis</i> sp.	?	UKY	?	GQ374626 ¹	GQ374708 ¹	GQ410705 ¹
<i>Aleiodes terminalis</i> Cresson	?	UKY	?	–	GQ374710 ¹	GQ410707 ¹
<i>Aleiodes pictus</i> (Herrich-Schäffer)	England	?	?	EF115464 ²	–	–
Ichneumonidae						
Acaenitinae						
<i>Spilopteron occiputale</i> (Cresson)	United States	CNC	CNC 422320	MK959483	MK851161	MK851398
<i>Coleocentrus rufus</i> Provancher	United States	CNC	CNC 422321	MK959401	MK851078	MK851315
Adelognathinae						
<i>Adelognathus</i> sp.	United States	CNC	CNC 422322	MK959374	MK851051	MK851288
Agriotypinae						
<i>Agriotypus armatus</i> Curtis	Czech Republic	CNC	CNC 422323	MK959376	MK851053	MK851290
Alomyinae						
<i>Alomya debellator</i> (Fabricius)	Switzerland	CNC	CNC 422374	MK959378	MK851055	MK851292
Anomaloninae						
Anomalonini						
<i>Anomalon picticorne</i> (Viereck)	United States	CNC	CNC 422324	MK959379	MK851056	MK851293
Gravenhorstiini						
<i>Therion texanum</i> (Ashmead)	United States	CNC	CNC 422325	MK959490	MK851168	MK851405
Ateleutinae						
<i>Ateleute</i> sp. nov.	United States	CNC	CNC 422344	MK959384	MK851061	MK851298
Banchinae						
Atrophini						
<i>Lissonota scutellaris</i> (Cresson)	United States	CNC	CNC 422326: (COI, 28S D2); CNC 422489: (EF1a)	MK959436	MK851113	MK851350

Taxa	Country of collection	Voucher depository	Voucher number	Genbank accession numbers		
				COI	28S D2	EF1a
Banchini						
<i>Exetastes bioculatus</i> Cresson	United States	CNC	CNC 422327	MK959424	MK851101	MK851338
Glyptini						
<i>Apophua simplicipes</i> (Cresson)	Canada	CNC	CNC 422328	MK959382	MK851059	MK851296
<i>Sphelodon phoxopteridis</i> (Weed)	United States	CNC	CNC 422329	MK959482	MK851160	MK851397
Brachycyrtinae						
<i>Brachycyrtus wardae</i> Bennett	Fiji	CNC	CNC 422490: (COI, 28S D2); CNC 422330: (EF1a)	MK959389	MK851066	MK851303
Campopleginae						
<i>Bathylectes infernalis</i> (Gravenhorst)	United States	CNC	CNC 422331	MK959388	MK851065	MK851302
<i>Campoletis sonorensis</i> (Cameron)	United States	CNC	CNC 422332	MK959391	MK851068	MK851305
<i>Campoplex</i> sp.	United States	CNC	CNC 422333	MK959392	MK851069	MK851306
<i>Casinaria grandis</i> Walley	United States	CNC	CNC 422334	MK959393	MK851070	MK851307
<i>Dusona egregia</i> (Viereck)	United States	CNC	CNC 422335	MK959415	MK851092	MK851329
<i>Hyposoter</i> sp.	United States	CNC	CNC 422336	MK959429	MK851106	MK851343
<i>Olesicampe</i> sp.	United States	CNC	CNC 422491: (COI, 28S D2); CNC 422337: (EF1a)	MK959452	MK851129	MK851366
<i>Rhimphoctona macrocephala</i> (Provancher)	Canada	CNC	CNC 422338	MK959474	MK851151	MK851389
Claseinae						
<i>Clasis</i> sp. nov.	Chile	CNC	CNC 422339	MK959398	MK851075	MK851312
Collyriinae						
<i>Collyria catoptron</i> Wahl	China	CNC	CNC 422340	MK959402	MK851079	MK851316
Cremastinae						
<i>Eiphosoma pyralidis</i> Ashmead	United States	CNC	CNC 422341	MK959418	MK851095	MK851332
<i>Xiphosomella setoni</i> Johnson	United States	CNC	CNC 422342	MK959496	MK851174	MK851411
Cryptinae						
Aptesini						
<i>Polytribax contiguus</i> (Cresson)	Canada	CNC	CNC 422349	MK959471	MK851148	MK851386
<i>Rhytura pendens</i> Townes	United States	CNC	CNC 422350	MK959477	MK851155	MK851393
Cryptini						
<i>Agonocryptus chichimecus</i> (Cresson)	United States	CNC	CNC 422343	MK959375	MK851052	MK851289
<i>Baryceros texanus</i> (Ashmead)	United States	CNC	CNC 422345	MK959386	MK851063	MK851300
<i>Diapetimorpha brunnea</i> Townes	United States	CNC	CNC 422346	MK959411	MK851088	MK851325
<i>Echthrus reluctator</i> (Linnaeus)	Germany	CNC	CNC 422348	MK959416	MK851093	MK851330
<i>Lymeon orbis</i> (Say)	United States	CNC	CNC 422347	MK959438	MK851115	MK851352
Ctenopelmatinae						
Ctenopelmatini						
<i>Ctenopelma sanguineum</i> (Provancher)	United States	CNC	CNC 422354	MK959405	MK851082	MK851319
<i>Xenoschisis limata</i> (Cresson)	United States	CNC	CNC 422355	MK959495	MK851173	MK851410
Euryproctini						
<i>Euryproctus sentinis</i> Davis	United States	CNC	CNC 422356	MK959423	MK851100	MK851337
<i>Mesoleptidea decens</i> (Cresson)	United States	CNC	CNC 422357	MK959443	MK851120	MK851357
Mesoleiini						
<i>Barytarbes honestus</i> (Cresson)	United States	CNC	CNC 422358	MK959387	MK851064	MK851301
<i>Himerta luteofacia</i> Leblanc	United States	CNC	CNC 422359	MK959427	MK851104	MK851341
Perilissini						
<i>Lathrolestes asperatus</i> Barron	United States	CNC	CNC 422360	MK959433	MK851110	MK851347
<i>Perilissus concolor</i> (Cresson)	United States	CNC	CNC 422361	MK959461	MK851138	MK851375
Pionini						
<i>Rhorus bartelti</i> Luhman	Canada	CNC	CNC 422362	–	MK851152	MK851390
<i>Sympherta fucata</i> (Cresson)	United States	CNC	CNC 281120	MK959487	MK851165	MK851402

Taxa	Country of collection	Voucher depository	Voucher number	Genbank accession numbers		
				COI	28s D2	EF1a
Scolobatini						
<i>Onarion</i> sp.	Bolivia	CNC	CNC 422365	MK959453	MK851130	MK851367
Seleucini						
<i>Seleucus cuneiformis</i> Holmgren	Japan	CNC	CNC 422364	MK959479	MK851157	MK851395
Westwoodiini						
<i>Westwoodia</i> sp.	Australia	CNC	CNC 422366	MK959493	MK851171	MK851408
Tribe indet.						
Ctenopelmatinae Genus NZ	New Zealand	CNC	CNC 422367	MK959406	MK851083	MK851320
Cyllocerinae						
<i>Cylloceria melancholica</i> (Gravenhorst)	United States	CNC	CNC 422368	MK959409	MK851086	MK851323
Diacritinae						
<i>Diacritus incompletus</i> Momi	Japan	CNC	CNC 422369	MK959410	MK851087	MK851324
Diplazontinae						
<i>Diplazon laetatorius</i> (Fabricius)	Canada	CNC	CNC 422370	MK959413	MK851090	MK851327
<i>Woldstedius flavolineatus</i> (Gravenhorst)	United States	CNC	CNC 422371	MK959494	MK851172	MK851409
Eucerotinae						
<i>Euceros</i> sp. nov.	United States	CNC	CNC 422372	MK959422	MK851099	MK851336
Hybrizontinae						
<i>Hybrizon rileyi</i> (Ashmead)	United States	CNC	CNC 422373: (COI, 28S D2); CNC 422392: (EF1a)	MK959428	MK851105	MK851342
Ichneumoninae						
Heresiarchini						
<i>Coelichneumon eximius</i> (Stephens)	United States	CNC	CNC 422378	MK959400	MK851077	MK851314
<i>Protichneumon grandis</i> (Brullé)	United States	CNC	CNC 422379	MK959473	MK851150	MK851388
Ichneumonini						
<i>Barichneumon neosorex</i> Heinrich	United States	CNC	CNC 422380	MK959385	MK851062	MK851299
<i>Cratichneumon w-album</i> (Cresson)	United States	CNC	CNC 422381	MK959403	MK851080	MK851317
<i>Orgichneumon calcatorius</i> (Thunberg)	United States	CNC	CNC 422382	MK959455	MK851132	MK851369
<i>Patroclodes montanus</i> (Cresson)	United States	CNC	CNC 422383	MK959459	MK851136	MK851373
Joppocryptini						
<i>Plagiotrypes concinnus</i> (Say)	United States	CNC	CNC 422384	MK959468	MK851145	MK851382
Listrodromini						
<i>Dilopharius otomitus</i> (Cresson)	United States	CNC	CNC 422385	MK959412	MK851089	MK851326
Phaeogenini						
<i>Centeterus euryptychiae</i> (Ashmead)	Canada	CNC	CNC 422375	MK959394	MK851071	MK851308
<i>Phaeogenes hebrus</i> (Cresson)	United States	CNC	CNC 422376	MK959464	MK851141	MK851378
<i>Stenodontus</i> sp. nov.	United States	CNC	CNC 422377	MK959484	MK851162	MK851399
Platylabini						
<i>Cyclolabus impressus</i> (Provancher)	United States	CNC	CNC 422386	MK959408	MK851085	MK851322
<i>Linytus exhortator</i> (Fabricius)	United States	CNC	CNC 422387	MK959435	MK851112	MK851349
Labeninae						
Orthognathelini						
<i>Grotea anguina</i> Cresson	United States	CNC	CNC 422388	MK959426	MK851103	MK851340
<i>Labium</i> sp.	Australia	CNC	CNC 422389	MK959432	MK851109	MK851346
Labenini						
<i>Apechoneura</i> sp.	Bolivia	CNC	CNC 422390	MK959380	MK851057	MK851294
<i>Labena grallator</i> (Say)	United States	CNC	CNC 422391	MK959431	MK851108	MK851345
Poecilocryptini						
<i>Poecilocryptus nigromaculatus</i> Cameron	Australia	? (28s); CNC (EF1a)	? (28s); CNC 422392 (EF1a)	–	AJ302921 ³	MK851383

Taxa	Country of collection	Voucher depository	Voucher number	Genbank accession numbers		
				COI	28S D2	EF1a
Lycoriniinae						
<i>Lycorina glaucomata</i> (Cushman)	United States	CNC	CNC 422393	MK959437	MK851114	MK851351
Mesochorinae						
<i>Astiphromma</i> sp. nov.	United States	CNC	CNC 422394	MK959383	MK851060	MK851297
<i>Chineater masneri</i> Wahl	Chile	CNC	CNC 422395	MK959395	MK851072	MK851309
<i>Cidaphus paniscoides</i> (Ashmead)	United States	CNC	CNC 422396	MK959397	MK851074	MK851311
<i>Lepidura collaris</i> Townes	Chile	CNC	CNC 422397	MK959434	MK851111	MK851348
<i>Mesochorus</i> sp.	United States	CNC	CNC 422398	MK959442	MK851119	MK851356
Metopiinae						
<i>Exochus semirufus</i> Cresson	United States	CNC	CNC 422399	MK959425	MK851102	MK851339
<i>Metopius pollinctorius</i> (Say)	United States	CNC	CNC 422400	MK959444	MK851121	MK851358
<i>Scolomus</i> sp.	Chile	CNC	CNC 422401	MK959478	MK851156	MK851394
<i>Seticornuta terminalis</i> (Ashmead)	United States	CNC	CNC 422402	MK959480	MK851158	MK851396
Microleptinae						
<i>Microleptes</i> sp.	South Korea	CNC	CNC 422403	MK959445	MK851122	MK851359
Neorhacodinae						
<i>Neorhacodes enslini</i> (Ruschka)	Spain	CNC	CNC 422434	MK959446	MK851123	MK851360
Nesomesochorinae						
<i>Chriodes</i> sp.	Madagascar	CNC	CNC 422404	MK959396	MK851073	MK851310
<i>Nonnus</i> sp.	Argentina	CNC	CNC 422405	MK959449	MK851126	MK851363
Ophioninae						
<i>Enicospilus flavostigma</i> Hooker	United States	CNC	CNC 422406	MK959420	MK851097	MK851334
<i>Hellwigia obscura</i> Gravenhorst	France	?	?	–	AJ302858 ⁴	–
<i>Ophion</i> sp.	United States	CNC	CNC 422407	MK959454	MK851131	MK851368
<i>Skiapus</i> sp.	Mozambique	CNC	CNC 422408	MK959481	MK851159	–
<i>Thyreodon</i> sp.	Guyana	CNC	CNC 422409	MK959492	MK851170	MK851407
Orthocentrinae						
<i>Megastylus</i> sp. nov.	United States	CNC	CNC 422410	MK959441	MK851118	MK851355
<i>Orthocentrus</i> sp.	United States	CNC	CNC 422411	MK959456	MK851133	MK851370
<i>Proclitus speciosus</i> Dasch	United States	CNC	CNC 422412	MK959472	MK851149	MK851387
Orthopelmatinae						
<i>Orthopelma mediator</i> (Thunberg)	Sweden	CNC	CNC 422413	MK959457	MK851134	MK851371
Oxytorinae						
<i>Oxytorus albopleuralis</i> (Provancher)	United States	CNC	CNC 422414	MK959458	MK851135	MK851372
Pedunculinae						
<i>Pedunculus</i> sp. nov.	Chile	CNC	CNC 422415	MK959460	MK851137	MK851374
Phygadeuontinae						
<i>Acrolyta</i> sp.	United States	CNC	CNC 422351	MK959372	MK851049	MK851286
<i>Endasys patulus</i> (Viereck)	United States	CNC	CNC 422352	MK959419	MK851096	MK851333
<i>Mastrus</i> sp.	United States	CNC	CNC 422353	MK959439	MK851116	MK851353
Pimplinae						
Delomeristini						
<i>Perithous divinator</i> (Rossi)	Canada	CNC	CNC 422416	MK959462	MK851139	MK851376
Ephialtini						
<i>Acrotaphus wiltii</i> (Cresson)	United States	CNC	CNC 422417	MK959373	MK851050	MK851287
<i>Clistopyga recurva</i> (Say)	United States	CNC	CNC 422418	MK959399	MK851076	MK851313
<i>Dolichomitus irritator</i> (Fabricius)	United States	CNC	CNC 422419	MK959414	MK851091	MK851328
<i>Zaglyptus pictilis</i> Townes	United States	CNC	CNC 422420	MK959498	MK851176	MK851413
Pimplini						
<i>Pimpla annulipes</i> Brullé	Canada	CNC	CNC 422421	MK959467	MK851144	MK851381
<i>Theronia bicincta</i> (Cresson)	United States	CNC	CNC 422422	MK959491	MK851169	MK851406

Taxa	Country of collection	Voucher depository	Voucher number	Genbank accession numbers		
				COI	28s D2	EF1a
Poemeniinae						
<i>Neoxorides caryae</i> (Harrington)	United States	CNC	CNC 422423	MK959447	MK851124	MK851361
<i>Poemenia albipes</i> (Cresson)	United States	CNC	CNC 422424	MK959469	MK851146	MK851384
Rhyssinae						
<i>Megarhyssa greeni</i> Viereck	Canada	CNC	CNC 422425	MK959440	MK851117	MK851354
<i>Rhyssa crevieri</i> (Provancher)	Canada	CNC	CNC 422426	MK959475	MK851153	MK851391
<i>Rhyssella nitida</i> (Cresson)	Canada	CNC	CNC 422427	MK959476	MK851154	MK851392
Sisyrostolinae						
<i>Brachyscleroma</i> sp.	Kenya	CNC	CNC 422428	MK959390	MK851067	MK851304
<i>Erythrodoilius calamitosus</i> Seyrig	Madagascar	CNC	CNC 422429	MK959421	MK851098	MK851335
Stilbopinae						
<i>Notostilbops</i> sp. nov.	Chile	CNC	CNC 422430	MK959450	MK851127	MK851364
<i>Stilbops vetulus</i> (Gravenhorst)	Hungary	CNC	CNC 422431	MK959486	MK851164	MK851401
Tatogastrinae						
<i>Tatogaster nigra</i> Townes	Chile	CNC	CNC 422432	MK959488	MK851166	MK851403
Tersilochinae						
<i>Allophrys divaricata</i> Horstmann	United States	CNC	CNC 422493: (COI, 28S D2); CNC 422433: (EF1a)	MK959377	MK851054	MK851291
<i>Peucobius fulvus</i> Townes	United States	CNC	CNC 422435	MK959463	MK851140	MK851377
<i>Phrudus</i> sp.	South Korea	CNC	CNC 422436	MK959465	MK851142	MK851379
<i>Stethantyx nearctica</i> Townes	United States	CNC	CNC 422437	MK959485	MK851163	MK851400
<i>Tersilochus</i> sp.	United States	CNC	CNC 422438: (COI, EF1a); CNC 422494: (28s D2)	MK959489	MK851167	MK851404
Tryphoninae						
Eclytini						
<i>Eclytus</i> sp.	United States	CNC	CNC 422495: (COI, 28S D2); CNC 422439: (EF1a)	MK959417	MK851094	MK851331
Idiogrammatini						
<i>Idiogramma longicauda</i> (Cushman)	United States	CNC	CNC 422440	MK959430	MK851107	MK851344
Oedemopsini						
<i>Zagryphus nasutus</i> (Cresson)	United States	CNC	CNC 422441: (COI, EF1a); CNC 422496: (28s D2)	MK959499	MK851177	MK851414
Phytodietini						
<i>Netelia</i> sp.	United States	CNC	CNC 422442	MK959448	MK851125	MK851362
<i>Phytodietus vulgaris</i> Cresson	United States	CNC	CNC 422443	MK959466	MK851143	MK851380
Tryphonini						
<i>Cteniscus</i> sp.	United States	CNC	CNC 422444	MK959404	MK851081	MK851318
<i>Cycasis rubiginosa</i> (Gravenhorst)	Switzerland	CNC	CNC 422445	MK959407	MK851084	MK851321
<i>Polyblastus</i> sp.	United States	CNC	CNC 422446	MK959470	MK851147	MK851385
Xordinae						
<i>Aplomerus</i> sp.	United States	UKY	CNC 681999 (COI, 28s D2), CNC 422447: (EF1a)	MK959381	MK851058	MK851295
<i>Odontocolon albotibiale</i> (Bradley)	United States	CNC	CNC 422497: (COI, 28s D2); CNC 422448: (EF1a)	MK959451	MK851128	MK851365
<i>Xorides stigmapterus</i> (Say)	Canada	CNC	CNC 422449	MK959497	MK851175	MK851412

Supplementary material 1

Ichneumonidae complete phylogenetic matrix, molecular characters coded as 0123

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: phylogenetic data (nexus format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl1>

Supplementary material 2

Ichneumonidae complete phylogenetic matrix, molecular characters coded as 0123

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: phylogenetic data (Hennig86 format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl2>

Supplementary material 3

Ichneumonidae phylogenetic matrix, molecular characters only, coded as ACGT

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: phylogenetic data (nexus format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl3>

Supplementary material 4

Ichneumonidae phylogenetic matrix, molecular characters only, coded as ACGT

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: phylogenetic data (Hennig86 format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl4>

Supplementary material 5

Total evidence parsimony trees

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: Phylogenetic trees (Winclada format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl5>

Supplementary material 6

Morphology-only parsimony trees

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: Phylogenetic trees (Winclada format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl6>

Supplementary material 7

Molecular-only parsimony trees

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: Phylogenetic trees (Winclada format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl7>

Supplementary material 8

Bayesian total evidence trees

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: Phylogenetic trees (Winclada format)

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Link: <https://doi.org/10.3897/jhr.71.32375.suppl8>

Supplementary material 9

Bayesian molecular-only trees

Authors: Andrew M.R. Bennett, Sophie Cardinal, Ian D. Gauld, David B. Wahl

Data type: Phylogenetic trees (Winclada format)

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