Systematic Entomology

Systematic Entomology (2009), **34**, 162–187

Description, circumscription and phylogenetics of the new tribe Zaeucoilini (Hymenoptera: Figitidae: Eucoilinae), including a description of a new genus

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Abstract. Neotropical eucoiline genera that have been included in and allied with the *Zaeucoila* genus group are redescribed. Following character analysis and phylogenetic reconstruction (25 taxa, 96 morphological characters, 1452 ribosomal and mitochondrial characters), this informal genus group was found to be monophyletic, and hence raised to formal recognition as a tribe of eucoilines, namely Zaeucoilini **new tribe**. Through phylogenetic reconstruction, *Aegeseucoela* Buffington was determined to be polyphyletic; the type species of *Aegeseucoela*, *A. grenadensis* (Ashmead), is transferred to *Agrostocynips* **comb.n.**; the orphaned species, *A. flavotincta* (Kieffer), is transferred to *Marthiella* Buffington **gen.n.**, **comb.n.** Based on the examination of the holotype of *Diranchis flavipes* Ashmead, 1900, this species is transferred to *Rhabdeucoela* **comb.n.**, where it is both a junior, subjective synonym of *flavipes* (Ashmead, 1894) **syn.n.** and a junior, secondary homonym. Zaeucoilini contains the following genera: *Agrostocynips* Diaz, *Dettmeria* Borgmeier, *Diceratastpis* Ashmead, *Lopheucoila* Weld, *Marthiella* Buffington, *Moneucoela* Kieffer, *Moritiella* Buffington, *Penteucoila* Weld, *Preseucoela* Buffington, *Rhabdeucoela* Kieffer, *Tropideucoila* Ashmead and *Zaeucoila* Ashmead. Characters and character states applicable specifically to Zaeucoilini are defined and illustrated. Characters supporting the monophyly of each genus are discussed. The plesiomorphic host for members of the Zaeucoilini are postulated as agromyzid leaf-mining Diptera, with one shift within the clade containing *Dettmeria*, *Diceratastpis* and *Lopheucoila* to fruit-infesting Diptera. New host records are reported for species of *Preseucoela*, *Rhabdeucoela* and *Zaeucoila*. All known hosts for the species of each genus are reported, as are known distributions and locations of type specimens.

Introduction

The Figitidae (Hymenoptera: Cynipoidea) are a lineage of cynipoid wasps parasitic on other holometabolous insects. The figitids are composed of the subfamilies Aspicerinae, Anacharitinae, Charipinae, Emargininae, Euceroptrinae, Eucoilinae, Figitinae, Parnipinae, Plectocynipinae, Pycnostigminae and Thrasorinae. A robust phylogeny of the figitids was produced by Buffington *et al.* (2007). Figitids are found in most habitats worldwide; a few subfamilies appear to be restricted to specific biogeographical regions (Euceroptrinae: Nearctic; Parnipinae: western Palearctic; Plectocynipinae: Neotropic; Pycnostigminae: Afrotropic) (Ronquist, 1999; Buffington & van Noort, 2007; Buffington, 2008; Buffington & Liljeblad, 2008).

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The Eucoilinae

The eucoiline wasps are endoparasitoids of cyclorrhaphous Diptera inhabiting a variety of habitats. These wasps are generally shiny black to dark reddish brown and range in

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size from 0.5 to 5 mm. Eucoilinae presently contains 85 genera and 973 species (J. Liljeblad, personal communication); Nordlander (1984) speculated that the actual species count for all figitids is probably approximately 24 000, the majority of which will be eucoilines. For a review of higher eucoiline classification schemes and history, see Nordlander (1982), Fontal-Cazalla *et al.* (2002) and Buffington *et al.* (2007). A review of the biology of Eucoilinae was provided by Ronquist *et al.* (2006) and Buffington & Ronquist (2006). Updated keys to Neotropical genera were provided by Buffington & Ronquist (2006), although several genera are missing as they were described subsequently (i.e. *Preseucoela* Buffington, *Moritiella* Buffington, *Aegeseucoela* Buffington). Keys to eucoilines of the Palearctic region are provided by Forshage & Nordlander (2008). Taxonomists interested in eucoiline identification should avoid using Weld (1952) and Dalla Torre & Kieffer (1910), as both of these keys focus on unreliable characters and an outdated classification scheme.

Nordlander (1982) summarized his previous 8 years of research by proposing informal genus groups defined by explicit morphological criteria. The groups defined by Nordlander (1982) were the *Gronotoma* group, *Trybliographa* group, *Rhoptromeris* group, *Chrestosema* group, *Ganaspis* group and the *Kleidotoma* group. The description of these genus groups was the first attempt to bring structure to eucoiline classification, although these hypotheses were not tested quantitatively until Fontal-Cazalla *et al.* (2002) provided an initial hypothesis of relationships between Eucoilinae and other subfamilies of Figitidae.

Nordlander (1982) included many of the taxa herein included in Zaeucoilini within the *Gronotoma* group of genera, i.e. *Rhabdeucoela* Kieffer, *Penteucoila* Weld, *Diceratastpis* Ashmead and *Zaeucoila* Ashmead. Diaz & Gallardo (1997) placed three of the Neotropical genera included originally in the *Gronotoma* group by Nordlander (1982) into a new group called the *Zaeucoila* group (these genera being *Rhabdeucoela*, *Penteucoila* and *Zaeucoila*); to this group, they added *Agrostocynips* Diaz, *Tropideucoila* Ashmead, *Lopheucoila* Weld, *Dettmeria* Borgmeier and *Moneucoela* Kieffer (Diaz & Gallardo, 1997, 1998; Gallardo & Diaz, 1999). Buffington (2002, 2004a, 2006) described three new genera and included them within the *Zaeucoila* group. Ronquist *et al.* (2006, table 10.4) reviewed all genera that had been included within the *Zaeucoila* group.

The present study is the first formal description of the Zaeucoilini **new tribe** and attempts to resolve difficulties in the identification of the included genera through redescriptions and generic circumscriptions based on synapomorphies provided by phylogenetic analysis. Members of the Zaeucoilini largely have a stout, compact habitus. Additionally, a number of variably sculptured structures are present on the mesoscutum and mesomesoscutellum; these areas are usually devoid of heavy sculpturing within eucoiline genera outside of the Zaeucoilini.

Most members of the Zaeucoilini also share a biological character: where known, except for *Lopheucoila*, *Diceratastpis* and *Dettmeria*, all members are koinobiont endoparasitoids of the dipterous leaf-mining flies in the family Agromyzidae. Apart from species within the Diglyphosemini *sensu* Forshage & Nordlander (2008) (all of which parasitize Agromyzidae; M. L. Buffington, unpublished), there are only two other eucoiline genera presently known to attack agromyzid flies, i.e. *Nordlandiella* Diaz (Valladares *et al.*, 1982; Buffington, 2004b) and *Weldia* Yoshimoto (Yoshimoto, 1962b). Agromyzid infestations are a general agricultural concern, often causing serious damage in several agroecosystems (Johnson, 1987). Eucoilines are frequently bred from agromyzids in the field (both agroecosystems and natural ecosystems) yet rarely identified past the subfamily rank (M. L. Buffington, personal observation).

Materials and methods

Material examined

The specimens used in this study are deposited in the following institutions: AEIC, American Entomological Institute, Gainesville, FL, U.S.A. (D. Wahl); ANEM, Museo Entomologico, Asociacion Nicaraguense de Entomologia, Nicaragua (J. Maes); CASC, California Academy of Sciences, San Francisco, CA, U.S.A. (R. Zuparko); CNCI, Canadian National Collection of Insects, Ottawa, Canada (J. Read); MLP, Museo de La Plata, La Plata, Argentina (N. Diaz); NHM; The Natural History Museum, London, U.K. (D. Notten); TAMU, Texas A&M University Insect Collection, College Station, TX, U.S.A. (E. Riley); UCRC, University of California at Riverside, Riverside, CA, U.S.A. (D. Yanega); USNM, United States National Museum (Smithsonian Institution), Washington, D.C., U.S.A. (M. Buffington); ZMHB, Museum für Naturkunde der Humboldtuniversität, Berlin, Germany (F. Koch).

Additional sources of specimens

Institutions and individuals who donated ethanol-preserved specimens for this study were: ANEM, CNCI, TAMU, UCRC; Dr Owen Lewis, Imperial College at Silwood Park, U.K. Large series of pinned specimens were obtained from the following institutions and individuals: AEIC, CASC, NHM, TAMU, USNM and Dr Sonja Scheffer (USDA, Beltsville, MD, U.S.A.). Voucher specimens of all taxa examined (except holotypes) are deposited at TAMU, UCRC and USNM (specimens labelled by MB).

Field collections

The primary means of collecting Zaeucoilini wasps is by use of a triangular-head sweepnet in various vegetation types. These wasps typically are not strong fliers or jumpers, so gently dragging the net along the ground, at approximately 15° off axis in the direction of sweeping, forces fleeing wasps into the net. Aspirating Zaeucoilini out

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of a sweepnet can be challenging; these wasps tend to 'duck and roll' to protect themselves, and often end up in the vegetation and duff at the bottom of the netbag. Disturbed wasps will eventually emerge and become active, at which time they can be captured. Open grassland and flowering annuals were best sources for the eucoilines examined in this study, but yellow pan traps and Malaise traps were also used with success.

Specimen preparation

All scanning electron micrograph (SEM) images utilized in this study were prepared digitally on a Phillips XL30 SEM (operated by the author and F. Fontal-Cazalla at the University of Uppsala, Sweden) or on a JOEL JSM-5600 SEM (operated by James Ehrman, Digital Microscope Facility, Mt. Allison University, Sackville, NB, Canada). Specimen preparation and dissection for the SEM followed the protocol outlined in Fontal-Cazalla *et al.* (2002). Light microscope images were obtained using techniques described in Buffington *et al.* (2005). The digital images are stored on MorphBank (www.morphbank.com). Collections of taxon images discussed here can be accessed through a Morphbank collection number at the end of each genus description.

Descriptive format

Descriptions are not included for *Agrostocynips*, *Moritiella* and *Preseucoela*; these genera and the species therein were treated by, respectively, Buffington & Scheffer (2008), Buffington (2006) and Buffington (2004a), in precisely the same format as the genera listed below.

Diagnoses focus on features that are recognizable easily by other observers, and closely related taxa that may have similar gross morphologies are distinguished. Some diagnostic features are unique combinations of characters, whereas others are autapomorphies found through phylogenetic analysis. Following each diagnosis is a generic circumscription based on synapomorphies recovered in the phylogenetic analysis. A discussion of these synapomorphies and their relative utility follow each generic treatment. A list of all valid species is included for each genus; those for which at least part of the type series was examined are indicated by an asterisk (*).

Phylogenetic analysis

Taxon sampling. When possible, the holotype of the type species of each genus was examined (Supporting Information SI1). For those genera presently analysed, as many described species as possible were examined. In those genera where some type material was unavailable (*Agrostocynips* and *Dettmeria*), undetermined species that could be assigned unequivocally to those genera were examined.

Outgroup exemplars. The outgroup choice was based on Buffington *et al.* (2007) and Buffington & Liljeblad (2008), in which the Diglyphosemini (Forshage & Nordlander, 2008) were recovered as a sister group to the clade containing all the Zaeucoilini + core Eucoilinae (Supporting Information SI3). Two diglyphosemines, *Disorygma pacifica* (Yoshimoto) and *Gronotoma micromorpha* (Perkins), were chosen as outgroup terminals.

Character coding

Morphological characters were obtained from the previous studies of Fontal-Cazalla *et al.* (2002) and Buffington *et al.* (2007); however, neither of these previous analyses was able to incorporate all genera of the Zaeucoilini. Males and females (if both genders were available) were examined for sexual dimorphism in each character state. A description of all the morphological characters can be found in Supporting Information SI2.

The SEM series for each genus allowed for simultaneous character and character state comparisons by placing images from up to ten taxa simultaneously on one computer screen. Coding was accomplished by comparing the SEMs of each genus with other genera, then coding (if possible) the taxa for which there was no SEM series by examining these taxa with the stereomicroscope. Additionally, certain characters and character states can be misinterpreted in SEM images; curated museum specimens were used to clarify these characters. Characters that were undiagnosable without the aid of the SEM (for those taxa in which an SEM series was not available) were coded as (?); characters that were inapplicable for certain taxa were coded as (–). Characters that showed variation across species within a genus were coded as polymorphisms.

Data analysis

The resulting data matrix contained 25 taxa and 1549 characters (96 morphological/biological, 1452 ribosomal/mitochondrial). The majority of the morphological data are binary characters. Of 14 multistate characters, all are treated as unordered. Sequence alignments used herein were based entirely on the structural model (Gillespie, 2004; Gillespie *et al.*, 2005) proposed for Cynipoidea (Buffington *et al.*, 2007) and included all gene regions. The structurally aligned, total-evidence matrix constructed for this analysis is based largely on Buffington *et al.* (2007). However, several key differences are present in this matrix. First, the 18S data partition is not included here because so few ingroup taxa are represented by this gene fragment; second, a reduced morphological character partition is used here, focusing on characters with phylogenetic information within the Diglyphosemini and Zaeucoilini the excluded characters from Buffington *et al.* (2007) being inapplicable to Eucoilinae. Genbank accession numbers for taxa and genetic data used herein are summarized in Supporting Information SI1. The

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final molecular and morphological matrix is available from Treebase (ID S2196). Sequence data is missing for *Moneucoela parvicupula* Keiffer, *Lopheucoila anastrephae* Weld and *Penteucoila triloris* Weld; for the sake of completeness, these taxa were included in all analyses although they were seriously deficient in character data. It is hoped that additional analyses of these taxa will be carried out in the future as molecular character data become available.

Data were analysed under parsimony in PAUP* (Swofford, 2002) using the following settings: tree bisection reconnection (TBR), start from random trees, 10 000 reps, swap on best only. The successive approximation method (Farris, 1969) was employed to focus the phylogenetic signal of the dataset; four rounds of successive approximation resulted in stable tree lengths. Bootstrap support values (Felsenstein, 1985) were calculated in PAUP* using 5000 replications of 100 rounds of TBR per replicate. Partitions for the Bayesian analysis were the following: RAA (region of ambiguous alignment), REC (regions of extension and contraction), STEM (stem regions characterized by Watson and Crick base pairing) [28S partition], COI (cytochrome oxidase I) position 1, 2 and 3 [COI partition] and morphology. The likelihood ratio test as performed using modeltest 3.06 (Posada & Crandall, 1998) was used to select a model of molecular evolution (for Bayesian analysis) for each data partition. The GTR model (Lanave *et al*., 1984; Tavaré, 1986), under the assumption that rates varied across sites according to a discrete gamma distribution with four rate categories (Γ; Yang, 1994), with a proportion of the sites invariable (I; Gu *et al*., 1995) was determined to be the best-fit model for each of the molecular partitions. The Markov-k model (Lewis, 2001), under the assumption that variable characters were sampled, was applied to the morphological/biological partitions and with rate variation modeled using the Γ distribution. Justification and a discussion of the use of morphological characters in a Bayesian framework are summarized in Buffington *et al*. (2007). All model parameters were allowed to be partition specific using a rate multiplier (Nylander *et al*., 2004). Analyses of MCMC (Markov chain Monte Carlo) were carried out using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck, 2003). Each analysis was continued for 10 million generations using 12 chains with default settings for prior distributions, proposal rates and proposal distributions. The chains were thinned by sampling every 1000th generation and two separate runs starting with random trees were completed for each dataset to help ensure stability was reached in the analyses (Huelsenbeck *et al*., 2002). The results of both runs were used to construct a majority-rules consensus tree; burn-in was set to 1000 trees after assessment of the log-likelihood scores in a spreadsheet program.

Terminology

This section is intended to define more clearly morphological terms and states encountered in the key to genera, the redescriptions of genera and the characters used in the phylogenetic analysis. Several important morphological features, such as the notauli, have been referred to in the literature by several different names [e.g. parapsidal grooves (Weld, 1952; Yoshimoto, 1962b); 'Parapsidenfurchen' (Dalla Torre & Kieffer, 1910); notauli (Nordlander, 1976; Quinlan, 1986, 1988)]. Hence, this section should help to stabilize morphological terms associated with eucoilines. Terminology of skeletal structures follows that of Harris (1979), Ronquist & Nordlander (1989) and Ronquist (1995).

Genal carina (GC, Fig. 1D–F). A sharp or sometimes blunt edge on the head posterior to the eye. Often referred to as 'cheeks margined' in literature. This edge often appears to interact with widened pronotal plates common in Zaeucoilini.

Genal space. Area between the gena (or genal carina, if present) and the posterior margin of the compound eye, bounded ventrally by the malar sulcus and dorsally by the vertex.

Orbital furrow (OF, Fig. 1B, reduced; C, well developed). A distinct groove originating at either the lateral ocellus or the lateral side of the torulus (depending on the taxon) and lining the inner orbit of the eye, terminating at the clypeal margin after fusing with or paralleling the malar sulcus. In *Rhabdeucoela*, the orbital furrow originates at the lateral ocellus, but runs ventrally across the face and does not line the inner orbit of the eye.

Ocellar hair patch (OHP, Fig. 1C, D). Dense patch of setae (or at least punctures corresponding to setal bases) ventral of the lateral ocellus and often within the space between the central and lateral ocellus.

Admedian clypeal furrow (CF, Fig. 1A). Shallow to medium deep linear impression present on the lower face, converging towards the midline of the head towards the clypeal margin.

Ventral clypeal margin (VM, Fig. 1C). Usually smooth and rounded, but in a few genera (e.g. *Agrostocynips*) this area is radically different, with a blunt conical protuberance.

Protuberance on malar space (PRO, Fig. 1B). At least a small pyramidal knob or point on the ventral margin of the malar space.

Malar sulcus (MS, Fig. 1B). A groove running between the ventral margin of the compound eye and the dorsolateral margin of the clypeus. Ranges from simple (only one groove present) to compound (several grooves present); when compound, often a distinct ridge is present between the various grooves.

Hypostomal carina (HC, Fig. 1E, F). In most eucoilines, this carina terminates at the posterior mandibular articulation; in several genera examined in this study, the carina terminates at a point dorsal and mesal to the posterior mandibular articulation.

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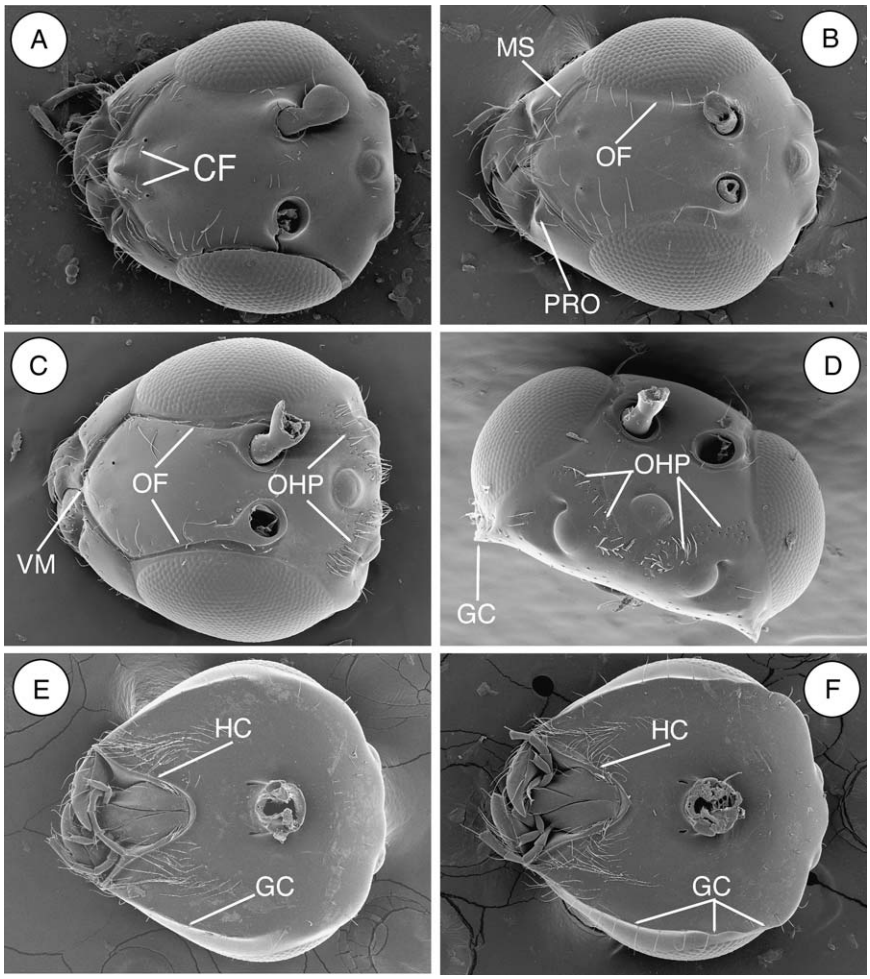

Fig. 1. (A–C) Head, anterior view: (A) *Gronotoma* sp., (B) *Agrostocynips diastrophi*, (C) *Tropideucoila* sp.; (D) head, dorsal view, *Tropideucoila* sp.; (E–F) head, posterior view: (E) *Agrostocynips diastrophi*, (F) *Zaeucoila unicarinata*. CF, clypeal furrows; GC, genal carina; HC, hypostomal carina; OF, orbital furrows; MS, malar sulcas; OHP, setal patches ventral of the lateral ocellus; PRO, pyramidal protuberances distal to the malar sulcas; VM, ventral margin of clypeus.

Pronotal plate (PP, Fig. 2A–C). Anterior, laterally margined aspect of the pronotum, often flattened and wide. The plate is divided into a posterior half (appears 'dorsal' in Fig. 2A–C) and an anterior half (appears 'ventral' in Fig. 2 A–C) by the lateral fovea (LF, Fig. 2A–C).

Lateral pronotal carina (LPC, Fig. 2A). A ridge, distinct from the pronotal plate, running from the dorsolateral corner of the pronotum ventrally to near the fore coxa; taxa possessing this feature often appear to have a large pronotal plate. This character is common in Diglyphosemini. The actual pronotal plate is quite small (Fig. 2A) and this carina should not be confused with the lateral margin of the true pronotal plate.

Pronotal ridge (R, Fig. 2B, reduced; C, well developed). Distinct to the reduced ridge lining the posterior aspect of the pronotal plate and running towards the anterior margin of the mesoscutum; in some species, several ridges may be observed in parallel.

Pronotal triangle (PT, Fig. 2C). A structure on the dorsal surface of the pronotum bound by two pronotal ridges laterally and the posterior margin of the pronotum anteriorly; found in genera with a well-developed pronotal ridge (e.g. *Tropideucoila*; Fig. 2C).

Pronotal impression (PRI, Fig. 2C). A wide impression running from the pronotal fovea of the pronotal plate to the posterior margin of the pronotum, most often aligned with the parascutal impression of the mesoscutum.

Lateral fovea (LF, Fig. 2A–C). Depression separating the anterior and posterior halves of the pronotal plate. The fovea can have either a closed state (where the fovea is not continuous with the lateral aspect of the pronotum; not

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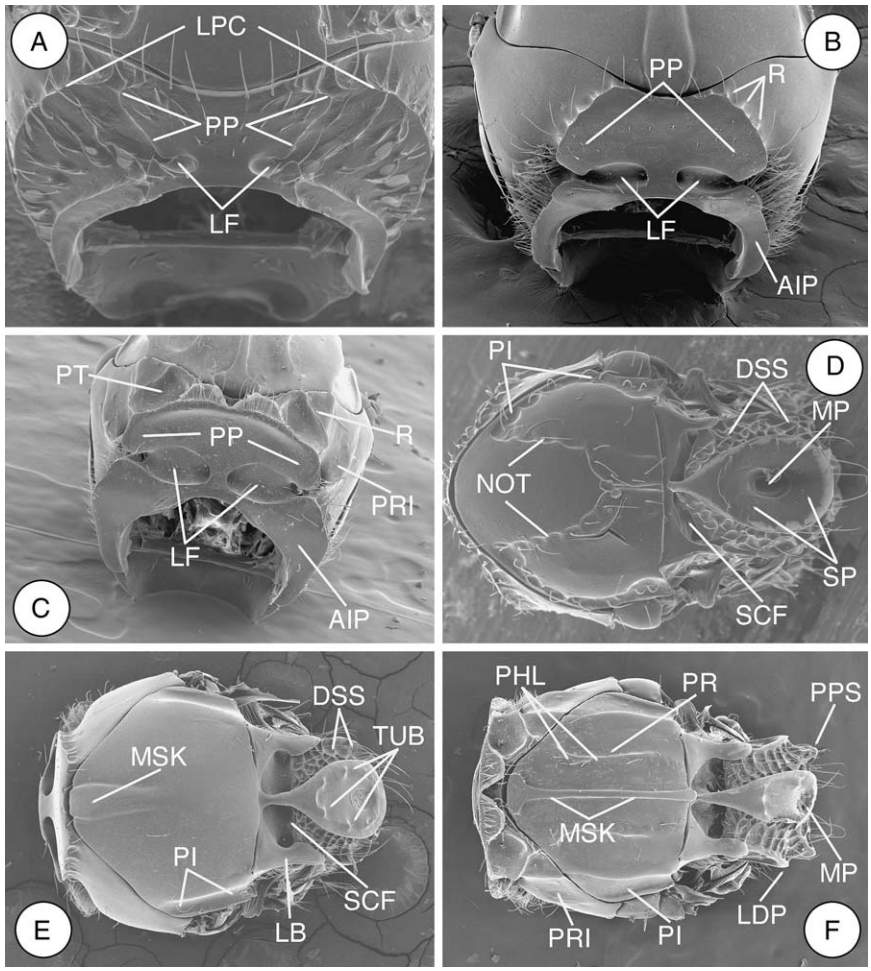

Fig. 2. (A–C) Mesosoma, anterodorsal view: (A) *Gronotoma* sp., (B) *Zaeucoila unicarinata*, (C) *Tropideucoila* sp.; (D–F) mesosoma, dorsal view: (D) *Gronotoma* sp., (E) *Zaeucoila unicarinata*, (F) *Tropideucoila* sp. AIP, anterior inflection of pronotum; DSS, dorsal surface of the mesoscutellum; LB, lateral bar; LDP, lateral–dorsal projections of the mesoscutellum; LF, lateral fovea of pronotum; LPC, lateral pronotal carina; MP, midpit of the scutellar plate; MSK, mesonotal keel; NOT, notaulices; PHL, parapsidal hair line; PI, parascutal impression; PP, pronotal plate; PPS, posterior projection of the mesoscutellum; PRI, pronotal impression; PR, parapsidal ridge; PT, pronotal triangle; R, pronotal ridge(s); SCF, scutellar fovea; SP, scutellar plate; TUB, tubercles of scutellar plate.

encountered in any genera studied in this analysis) or an open state (where the fovea is continuous with the lateral aspect of the pronotum).

Anteroventral inflection of pronotum (AIP, Fig 2B, C). Anterior part of pronotum, ventral to pronotal plate, that interacts with the posterior margin of the head. This inflection tends to be wider in taxa whose heads are flat along the posterior margin. This inflection can either be distinct from the anterior portion of the pronotal plate or fused with it.

Notaulus (NOT, Fig. 2D). Paired stucture of the mesoscutum, ranging from a deep, continuous or slightly punctate line to a very shallow, mere indication of a line extending from the anterior to the posterior margin of the mesoscutum. In taxa with a reduced notauli, only the anterior and posterior ends are visible. Notauli have also been referred to as parapsidal grooves (e.g. Weld, 1952). Absent in Zaeucoilini, notauli are common within the Diglyphosemini.

Medial mesoscutal keel (MSK, Fig. 2E, reduced; F, well developed). Ranging from a distinct structure continuous from the anterior to the posterior margins of the mesoscutum (Fig. 2F) to present only anteriorly (often with a great degree of variability) (Fig. 2E). Not to be confused with the confluence of the notaulae, as evidenced by Fig. 2D.

Parapsidal ridge (PR, Fig. 2F). Paired structure, present as a broad elevation parallel to the median mesoscutal keel; moderately to densely setose. Taxa possessing these ridges have been referred to as possessing '1–5 Längskielen' in addition to 'Parapsidenfurchen' (Dalla Torre & Kieffer,

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1910); it is not clear whether or not Dalla Torre & Kieffer (1910) were referring to 'parapsidal furrows' or the parapsidal signum (Ronquist & Nordlander, 1989) in their use of 'Parapsidenfurchen'. I prefer to use the term employed by Weld (1952), parapsidal ridges, because they are distinct ridges (not furrows) and are present on the parapsides of the mesoscutum.

Parapsidal hair line of mesoscutum (PHL, Figs 2F, 3C). Row of setae lining the parapsidal ridge or lining an area corresponding to the location of the parapsidal ridge (if the ridge is absent).

Parascutal impression (PI, Fig. 2D, E). Present in two forms. In the complete form, the impression extends from the lateroposterior margin of the mesoscutum anteriorly to the point of origin of the notaulus, essentially lining the lateral margin of the mesoscutum (PI, Fig. 2D). In the incomplete form, the impression extends from the lateroposterior margin of the mesoscutum anteriorly, ending at a point far removed from the anterior margin of the notaulus (in taxa that lack notauli, at least at the position where the notauli would normally be located), close to the widest point of the mesoscutum (when viewed dorsally) (PI, Fig. 2E).

Scutellar fovea (SCF, Fig. 2D, E). Paired structure resulting in the division of the scutoscutellar sulcus by the anterior septum of the scutellar plate; narrow to wide obliquely angled linear to semicircular impressions.

Scutellar plate (SP, Fig. 2D). A unique structure found in all Eucoilinae. The dorsal-most part of the mesomesoscutellum is modified into a large to small plate; a glandular release pit is located towards the posterior of the plate. The function of the plate and its associated pit is presently unknown. Dissections by the author have revealed that a large gland is present beneath the surface of the plate, with tubular ducts leading to pores within the pit of the plate (M. L. Buffington, personal observation).

Scutellar midpit (MP, Fig. 2D, F). Often also referred to as the 'glandular release pit' of the scutellar plate. The centre of the pit is perforated with glandular release pores, as revealed by SEM; presumed point of release of glandular secretions produced below the scutellar plate.

Scutellar tubercular projections (TUB, Figs 2E, 3B). Small tubercles present along the rim of the scutellar plate. These tubercles often each bear a seta, and give the scutellar plate a 'sawtooth' appearance when viewed laterally.

Dorsal surface of mesoscutellum (DSS, Fig. 2D, E). Portion of the mesoscutellum that is not obscured by the scutellar plate (in dorsal view); ranging in eucoilines from smooth to striate to heavily rugose.

Laterodorsal (LDP, Figs 2F, 3C) and posterior projections (PPS, Figs 2F, 3C) of mesoscutellum. Common in Zaeucoilini, these projections can either occur separately (e.g. *Diceratapsis*) or together (e.g. *Tropideucoila*), resulting in a maximum of four distinct projections from the posterior margin of the mesomesoscutellum.

Lateral bar of mesoscutellum (LB, Fig. 2E). A structure joining (but not fusing) the dorsal surface of the mesoscutellum with the axilla, above the scutoscutellar sulcus. In Zaeucoilini, the ventral portion of the lateral bar is expanded, resulting in a distinctly sinuate posterior margin.

Mesopleural triangle (MPT, Fig. 3A, C). An impressed area more or less in the middle of the mesopleuron. The 'base' of the triangle is aligned with the pronotal–mesopleural suture line; the 'hypotenuse' of the triangle extends from the ventral margin of the subalar pit to the middle of the pronotal–mesopleural suture line (the ventral endpoint of the base of the traingle); the 'axis' of the triangle extends from the dorsal margin of the subalar pit and extends to the dorsal endpoint of the pronotal–mesopleural suture line (also the dorsal endpoint of the base of the triangle). The dorsal ('axis') and ventral ('hypotenuse') margins of the triangle range from distinctly impressed to rounded and only slightly impressed.

Subalar pit (SAP, Fig. 3A). Distinct impression at posterior end of the mesopleural triangle; can open either obliquely anteriorly or straight laterally.

Mesopleural carina (MSC, Fig. 3A). Simple to slightly compound carina that extends from the anterior to the posterior margin of the mesopleuron.

Precoxal carina of mesopleuron (PCC, Fig. 3B, C). Carina that separates the lower part of the mesopleuron (below the mesopleural carina) from the mesosubpleuron.

Surcoxal depression (SD, Fig. 3B, C). A large, often carinate depression at the anterior point of origin of the precoxal carina; in some taxa, a second surcoxal depression is present at the posterior terminus of the precoxal carina (above the mesocoxa).

Posterior carina of mesosubpleuron. A narrow to wide carina that connects the medial edges of the mesocoxal rims along the posterior margin of the mesosubpleuron.

Metapectal–propodeal complex (Fig. 3A–D in part). An area where a great deal of fusion between sclerites has taken place, often resulting in extremely reduced forms in more derived eucoilines. Within the Zaeucoilini, gaps are often present at the anterior margin of the metapleuron (at its junction with the mesopleuron); these are the anterior impressions of the metepimeron (dorsal gap) and metepisternum (ventral gap).

No claims to original US government works

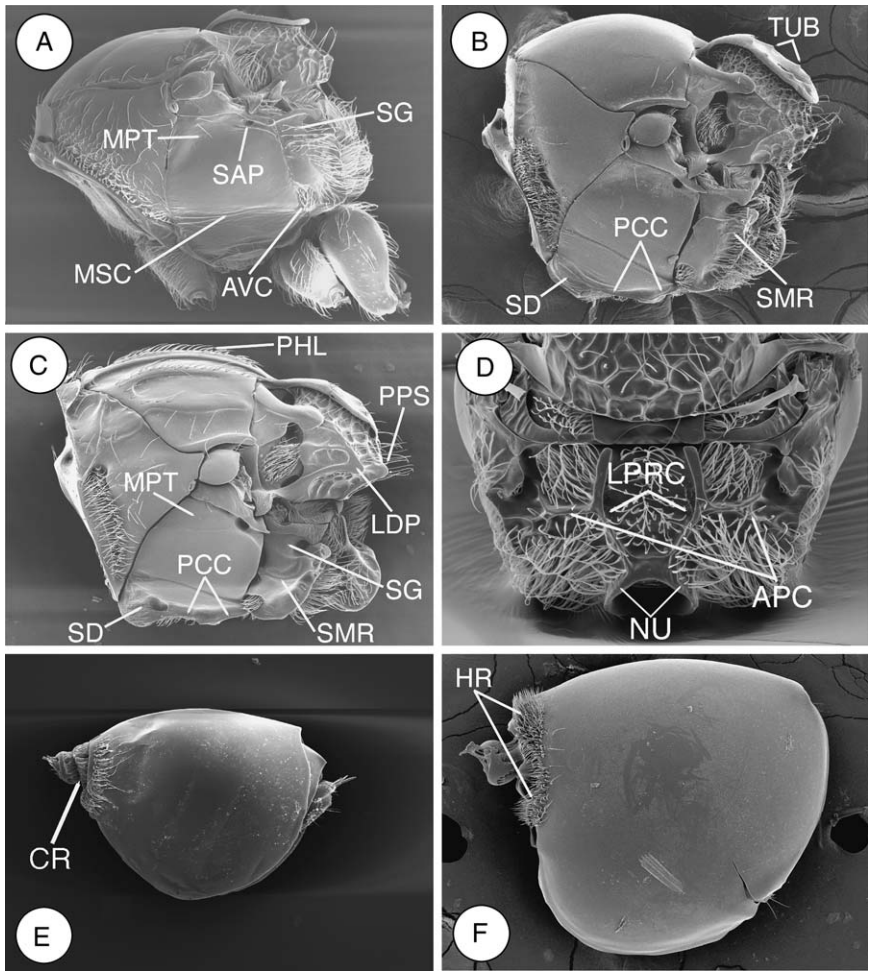

Fig. 3. (A–C) Mesosoma, lateral view: (A) *Disorygma depile*, (B) *Agrostocynips diastrophi*, (C) *Tropideucoila* sp.; (D) mesosoma, posterodorsal view, *Gronotoma* sp.; (E–F) mestasoma, lateral view: (E) *Gronotoma* sp., (F) *Zaeucoila unicarinata*. APC, auxillary propodeal carinae; AVC, anteroventral cavity; CR, crenulate ring; HR, hairy ring of metasoma; LDP, laterodorsal projections of the mesoscutellum; LPRC, lateral propodeal carinae; MPT, mesopleural triangle; MSC, mesopleural carina; NU, nucha; PCC, precoxal carina; PHL, parapsidal hair line; PPS, posterior projection of the mesoscutellum; SAP, subalar pit; SD, surcoxal depression; SG, spiracular groove; SMR, submetapleural ridge; TUB, tubercles of the scutellar plate.

Anteroventral cavity (AVC, Fig. 3A). A small, deep depression at the ventral end of the anterior impression of the metepimeron; commonly setose.

Spiracular groove (SG, Fig. 3A, C). Groove leading from the dorsoanterior margin of the metapleuron to the propodeal spiracle; often greatly enlarged in some genera (e.g. *Rhabdeucoela*).

Submetapleural ridge (SMR, Fig. 3B, C). A distinctly curved ridge extending from the ventral margin of the spiracular groove to the anterior margin of the metapleuron.

Lateral propodeal carina (LPRC, Fig. 3D). Paired structure; ridge-like carina that runs from the ventral margin of the mesoscutellum (or a point near to the ventral margin of the mesoscutellum), along the dorsal margin of the metapectal–propodeal complex, to the nucha.

Auxiliary propodeal carina (APC, Fig. 3D). A thin carina running from the posterior margin of the metapleuron to the lateral propodeal carina.

Nucha (NU, Fig. 3D). The ring-like structure projecting posteriorly from the propodeum that receives the petiole of the metasoma.

Crenulate ring of metasoma (CR, Fig. 3E). An abruptly widened posterior part of the petiole.

Hairy ring of metasoma (HR, Fig. 3F). Composed usually of dense setae, occasionally of several distinct lengths.

In most eucoiline genera, the hairy ring is 'complete', i.e. the setae extend from the dorsal to the ventral ends of the third abdominal terga (Fig. 3F). In a few genera the setal pattern is either highly reduced or lacking (e.g. *Gronotoma*, Fig. 3E).

Extent of R_1 of wings (Fig. 4A, B). Nordlander (1976) revealed that a great deal of taxonomic confusion was created in eucoiline systematics by the character 'closed versus open marginal cell'. For the vast majority of eucoilines, this feature is extremely variable (due to varying levels of pigmentation in the R_1 vein). In some members of the Zaeucoilini, however, the 'open marginal cell', i.e. R_1 not tubular along the anterior margin of the wing, is quite constant and an important feature for diagnosis. In the phylogenetic analysis, only taxa in which the R_1 vein is absent (Fig. 4B) were coded as having an open cell (state 1). Taxa that possessed an unpigmented R_1 vein (the latter resulting in a 'false' open cell; Fig. 4A) were coded as having a closed cell (state 0).

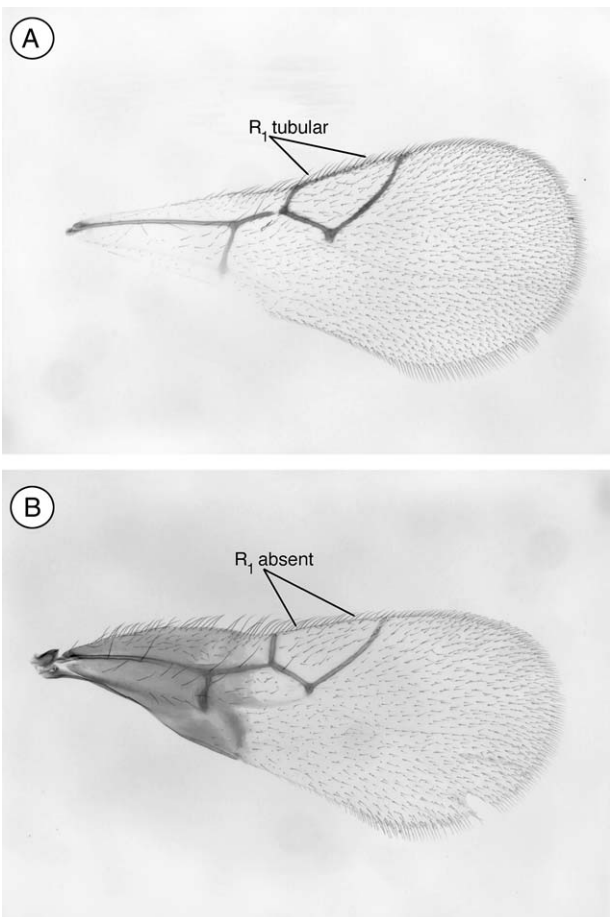

Fig. 4. (A, B) Forewings of Diglyphosemini and Zaeucoilini: (A) *Gronotoma* sp., (B) *Tropideucoila* sp. R_1 tubular results in a closed marginal cell; R_1 absent results in an open marginal cell.

Results

Zaeucoilini Buffington, new tribe

Type genus. *Zaeucoila* Ashmead, 1903

Diagnosis. Pronotal plate wide, at least half width of mesoscutum when seen in anterior view. This single autapomorphy for the group easily distinguishes any member of this tribe from any other eucoiline. The following is a list of characters and the genera that possess them that are also unique within Eucoilinae: orbital furrows present along inner margins of eyes (reduced to absent in *Agrostocynips*); parapsidal ridges present on mesoscutum (*Tropideucoila*, *Penteucoila*, *Dettmeria*, *Lopheucoila*); parapsidal hair lines present (*Tropideucoila*, *Penteucoila*, *Dettmeria*, *Lopheucoila*, *Marthiella*); mesoscutal keel present (*Tropideucoila*, *Penteucoila*, *Dettmeria*, *Lopheucoila*, *Moneucoela*, *Zaeucoila*); laterodorsal and/or posterior projections of the mesoscutellum present (all genera except *Agrostocynips*); and distinct genal carina (present in *Agrostocynips*, but limited to ventral half of gena). Members of the Zaeucoilini are most easily confused with members of the Digplyphosemini, especially *Ganaspidium* spp. However, all other members of the Eucoilinae have a narrow pronotal plate. *Ganaspidium* also possess a conical protuberance on the anterior margin of the clypeus; no zeucoiline has this character state, although conical protuberances are common on ventral of the malar sulcus in *Agrostocynips*, *Marthiella* and *Zaeucoila*.

Description. Predominantly black wasps, with occasionally yellow to brownish legs; cuticle shiny. Female antenna with 13 flagellomeres, male with 15 flagellomeres. Orbital furrows nearly always present, running at least from dorsal margin of inner orbit of eye to malar sulcus (occasionally from lateral ocellus base of mandible). Pronotal plate wide, at least half as wide as mesoscutum; lateral aspect of pronotum frequently ridged/sculptured. Mesoscutum ranging from completely smooth to sculptured with paired parapsidal ridges; parapsidal hair lines sometimes present; mesoscutal keel sometimes present. Mesopleural carina complete; mesopleural triangle frequently present. Mesoscutellar disk frequently with posterior and/or lateral projections; disk of mesoscutellum frequently with several small tubercles to a single conical projection dorsally. Base of metasoma always with complete hairy ring.

Key to genera of Zaeucoilini

Correct lighting is essential in the examination of eucoilines; glare will prevent the correct diagnosis of several features presented here. The user of this key should employ either fibre optic lamps in conjunction with light-dispersing plastic film, or use fluorescent lamps (which have natural light-dispersing properties).

No claims to original US government works

1. Parascutal impression present, complete (PI, Fig. 2D). Notauli present (NOT, Fig. 2D). Base of metasoma without hairy ring (Fig. 3E). Some species lack parascutal impression and notauli and possess hairy ring on metasoma (*Ganaspidium* spp.); these species all possess prominent solitary conical protuberances on ventral margins of clypeus and malar space ..... **Diglyphosemini**
– Parascutal impression always present, incomplete (PI, Fig. 2E, F). Notauli always absent (Fig. 2E, F). Hairy ring present at base of metasoma (Fig. 3F). Solitary conical protuberances occasionally on malar space, never on ventral margin of clypeus **2**
2. Pronotal plate wide, at least as half as wide as mesoscutum in anterior view (PP, Fig. 1B, C). Genal carina often present (GC, Fig. 1D–F). Mesoscutal keel often present (MSK, Fig. 2F). Laterodorsal projections and/or posterior projections of mesoscutellum present (LDP, PPS, Fig. 2F) or absent. Orbital furrows often present (OF, Fig. 1B, C) ..... **Zaeucoilini**, **3**
– Pronotal narrow, maximally one-third width of mesoscutum in anterior view (PP, Fig. 2A). Genal carina always absent. Mesoscutal keel always absent. Laterodorsal projections absent (a few taxa may possess either posterior projections of mesoscutellum or single posterior projection). Orbital furrows usually absent. ..... **'Core' Eucoilinae**
3. Posterior margin of mesoscutellum rounded, occasionally with reduced laterodorsal projections (Figs 2E, 3B) **4**
– Posterior margin of mesoscutellum not rounded, but with distinct, paired, posterior and/or laterodorsal projections (LDP, PPS, Figs 2F, 3C) **9**
4. Genal carina always present, sometimes restricted to ventral third to half of head **5**
– Genal carina absent ..... ***Preseucoela***
5. Genal carina reduced (visible only along ventral margin of malar space). Mesoscutal keel absent **6**
– Genal carina prominent, extending from ventral margin of malar space to dorsal part of head. Mesoscutal keel present, at least anteriorly **7**
6. Scutellar plate, when seen in profile, with distinct serrated 'sawtooth' appearance as a result of posteriorly directed denticles. Orbital furrows entirely lacking ..... ***Moritiella***
– Scutellar plate, when seen in profile, with distinct denticles, but not directed posteriorly. Orbital furrows present along inner margins of eyes ..... ***Agrostocynips***
7. Space anterior to genal carina dimpled. Orbital furrows removed from inner margins of eyes, extending across lower face and originating dorsally from lateral ocelli. Lateral propodeal carinae raised into blunt protuberances at junction with auxiliary propodeal carinae. Mesoscutellum in lateral view meeting scutellar plate at a 90° angle ..... ***Rhabdeucoela***
– Space adjacent to genal carina smooth. Orbital furrows present along inner orbits of compound eyes, not converging strongly across lower face, and not originating dorsally at lateral ocelli. Lateral propodeal carinae without protuberances. Mesoscutellum in lateral view meeting scutellar plate at distinctly acute angle **8**
8. Dorsal margin of pronotal plate crested, deeply bifurcate (as in Fig. 2C). Laterodorsal projections of mesoscutellum occasionally present, usually reduced. Marginal cell of wing always open. Parapsidal hair line (PHL, Figs 2F, 3C) present. Orbital furrows often extending to lateral ocelli. Genal carina present, often flanged posterior to compound eye ..... ***Marthiella***
– Dorsal margin of pronotal plate not crested (occasionally slightly bifurcate) (as in Fig. 2B). Laterodorsal projections of mesoscutellum always absent. Marginal cell of forewing always closed (pigmentation may vary). Parapsidal hair lines absent. Orbital furrows not extending to lateral margins of lateral ocelli. Genal carina present, not flanged ..... ***Zaeucoila***
9. Mesoscutal keel prominent; parapsidal ridge distinct (PR, Fig. 2F). Genal carina always present. Pronotal triangle (PT, Fig. 2C) large, with lateral side issuing from near laterodorsal margin of pronotal fovea. Pronotal impression present (PRI, Fig. 2C, F) **10**
– Mesoscutal keel present or absent; parapsidal ridge absent (Fig. 2E). Genal carina present or absent. Pronotal triangle small, with lateral side issuing from point mesal to laterodorsal margin of pronotal fovea. Pronotal impression absent **11**
10. Mesoscutal keel absent. Posterior projections of mesoscutellum elongate; laterodorsal projections of mesoscutellum significantly smaller or absent. Orbital furrows joining with malar sulcus at clypeal margin, far from compound eye. Ventral margin of mesopleural triangle rounded, indistinct (MPT, Fig. 3A) ..... ***Diceratastpis***
– Mesoscutal keel present. Posterior and laterodorsal projections of mesoscutellum equally developed, resulting in four distinct lobes in dorsal view. Orbital furrows joining malar sulcus at ventral margin of compound eye. Ventral margin of mesopleural triangle distinct (MPT, Fig. 3C) ..... ***Moneucoela***
11. Wings nearly devoid of setae, instead having small dots where setae generally are located. Metasoma slightly larger than mesosoma. Parasitoids of fruit-infesting cyclorrhaphous Diptera **12**
– Wings setose (basally bare in some species, but at least apically setose). Metasoma subequal in size to mesosoma. When known, parasitoids of Agromyzidae **13**
12. Scutellar plate with distinct spine overhanging midpit. Base of syntergum of metasoma with distinct dorsoventral impression in lateral aspect. R_1 of forewing not reaching anterior margin of wing. ..... ***Lopheucoila***
– Scutellar plate without spine. Base of syntergum of metasoma without dorsoventral impression. R_1 of forewing reaching anterior margin of wing ..... ***Dettmeria***
13. Scutellar plate with distinct spine overhanging midpit. Orbital furrows extending to lateral ocelli ..... ***Penteucoila***
– Scutellar plate without spine overhanging midpit (small tubercles often present). Orbital furrows extending only to lateral margins of toruli ..... ***Tropideucoila***

No claims to original US government works

Genera of Zaeucoilini

Agrostocynips Diaz

Agrostocynips Diaz, 1976: 32. Type species: *Agrostocynips clavatus* Diaz, 1976: 32, by original designation.

Aegeseucoela Buffington, 2002. Type species: *Aegeseucoela grenadensis* (Ashmead) **syn.n.**

Diagnosis. Genal carina reduced. Orbital furrows reduced to absent. Mesoscutal keel absent. Scutellar plate with distinct tubercles present. Most easily confused with *Zaeucoila*, which has a complete genal carinae, a mesoscutal keel present (at least anteriorly) and distinct orbital furrows.

Included species.

A. clavatus Diaz, 1976: 32. Holotype in MLP.
**A. diastrophi* (Ashmead), Buffington (2004). *Ganaspis diastrophi* Ashmead, 1896: 184–185. Holotype in USNM (#3280).
A. enneatoma (Diaz), Diaz & Gallardo (1997). *Zaeucoila enneatoma* Diaz, 1975: 1999. Holotype in MLP.
A. grenadensis* (Ashmead) **comb.n. *Diranchis grenadensis* Ashmead, 1900: 248. Holotype in NHM.
**A. robusta* (Ashmead), Buffington (2004). *Chrestosema robusta* Ashmead, 1894: 68. Holotype in USNM (#2336).

Distribution. Neotropical region: Brazil (*A. enneatoma*; Diaz & Gallardo, 1997), Argentina (*A. clavatus*; Diaz & Valladares, 1979); Nearctic region: southern Canada (British Columbia) (*A. diastrophi*) and continental U.S.A. (*A. diastrophi, A. robusta*) (Buffington & Scheffer, 2008). I have also seen undescribed species of *Agrostocynips* from Central Mexico, Chile and Columbia.

Biology. *Agrostocynips clavatus* has been recorded in the Neotropics from several agromyzid species in the genera *Melanagromyza* Hendal (De Santis *et al*., 1976) and *Liriomyza* Mik (Diaz & Valladares, 1979; A. Salvo, personal communication). Nearctic species of *Agrostocynips* have been reared from agromyzids in *Agromyza* Fallén [on *Panicum* (Poaceae)], *Liriomyza* (several host plants) and from *Phytomyza* Fallén (on *Ilex cassine* L. and *I. myrtifolia* Walter) (Buffington & Scheffer, 2008).

Remarks. *Agrostocynips* is closely related to *Zaeucoila*, differing in some reduced character states. The incomplete genal carina is a striking feature, more readily visible when the head is separated from the mesosoma; the incomplete state is distinctive from *Zaeucoila* (complete state) and *Preseuceola*, *Diceratastpis* (genal carina absent). The reduced orbital furrow is a constant character in *Agrostocynips*, but some species of *Zaeucoila* have gained this state in parallel. The presence of erect setae medially on the apical segment of the maxillary palp is unique within the Zaeucoilini, but common in Diglyphosemini; additionally, this feature is only visible in the SEM, and more species of *Agrostocynips* need to be surveyed for these setate to be confirmed as a definitive synapomorphy of the genus. The complete reduction of the mesonotal keel is an important feature of *Agrostocynips*, both taxonomically and phylogenetically. Unfortunately, some species in this group seem to grade between a rather apparent mesoscutal keel (leaning towards *Zaeucoila*) to an extremely reduced mesoscutal keel (leaning towards *Agrostocynips*); using other features (e.g. genal carina and orbital furrows) in combination with the mesoscutal keel helps to remedy this situation. Morphbank image collection: 270801.

Dettmeria Borgmeier

Dettmeria Borgmeier, 1935: 110. Type species: *Dettmeria rubiventris* Borgmeier, 1935: 111, by original designation.

Diagnosis. Similar to *Lopheucoila* in general appearance, but easily separated by the absence of a tooth overhanging the midpit of the scutellar plate, the forewing R_1 vein reaching the anterior margin of the wing, the base of the syntergum without dorsoventral impressions, and the posterior projections of the mesoscutellum distinct and well separated (joined in *Lopheucoila*).

Redescription

Head. Nearly glabrous with a few scattered setae along lower face, clypeus and malar space. Ocellar hair patch present. Ventral quarter of lower face with admedial clypeal furrows converging towards clypeus. Orbital furrows originating at lateral margin of torulus, merging with malar sulcus at ventral margin of compound eye. Malar sulcus simple. Malar space smooth; lacking protuberances. Genal carina present from ventral margin of malar space to dorsal margin of compound eye; slightly flanged in parts lateral to compound eye.

Antenna. Female: 13 segments, subfiliform with segments towards base moniliform; slightly clavate with segments becoming increasingly wider and shorter towards apex, apical segment longest; rhinaria present on segments 4–13. Male: 15 segments, moniliform; rhinaria on segments 3–15; segments 3–15 subequal in length; segment 3 modified, equal in length to segment 4, curved outwardly, excavated laterally.

Pronotum. Pronotal plate wide; dorsally crested, bifurcate, glabrous; pronotal fovea open. Pronotal triangle present. Pronotal impression present. Lateral pronotal carina absent. Lateral portion of pronotum (ventral to pronotal triangle) smooth and glabrous.

Mesoscutum. Mostly glabrous. Mesoscutal keel prominent, continuous across entire mesoscutum. Parapsidal ridges somewhat flattened; parapsidal hair lines present. Parascutal impression incomplete, broad, with a distinct dorsal border appearing as a 'second' pair of parapsidal

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ridges; aligned with pronotal impression anteriorly. Notauli absent.

Mesopectus. Upper part and lower part of mesopleuron smooth and glabrous. Dorsal and ventral margins of mesopleural triangle clearly defined. Mesopleural carina simple. Lower part of mesopleuron bounded by a reticulate precoxal carina; surcoxal depression present, reticulate.

Mesoscutellum. Scutellar plate small; midpit placed between centre point of plate and posterior margin of plate; rim of plate translucent; tubercles absent. Dorsal surface reticulate, margined laterally and posteriorly. Laterodorsal and posterior projections present. Lateral bars slightly longer than wide, ventral lobe present. Scutellar fovea large, nearly circular, smooth and deep.

Metapectal–propodeal complex. Metapectus entirely glabrous with a few setae present in spiracular groove. Spiracular groove deep with defined dorsal and ventral margins. Posterior margin of metapectus ridged. Metapleural ridge present, ultimately dividing into three ridges: one continuing ventrally, one directed anteriorly and one directed posteriorly, with deep foveae between ridges. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity oval and setose. Propodeum covered in long, erect setae. Lateral propodeal carinae nonparallel, strongly bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carina reduced. Nucha partially setose, slightly strigose.

Wings. Hyaline, with base of wing often darkened; glabrous except for apical fringe. R_1 incomplete; marginal cell slightly longer than deep. Apical fringe present, short.

Legs. Fore and mid coxa subequal in size, hind coxa twice the diameter of either fore or mid coxa. Fore coxa variously setose; mid coxa with anterior and lateral dorsoventral setal bands; hind coxa with lateral and posterior dorsoventral setal bands. Femora and tibiae with sparse setal lines; tarsomeres with dense, appressed setae. Length of hind tarsomere 1 equal to combined length of remaining hind tarsomeres.

Metasoma. Female: conspicuously larger than mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, hairs all of one length, interrupted apically; remainder of metasoma glabrous. Micropunctures present on posterior third of syntergum and on remaining terga. Terga posterior to syntergum gently angled ventrally, resulting in a 70° angle between syntergum and remaining terga. Male: as in female, but with terga posterior to syntergum abruptly angled ventrally, resulting in a 90° angle between syntergum and remaining terga.

Included species

D. euxestae Borgmeier, 1935: 112. Holotype in Instituto Biologia Vegetal, Rio de Janeiro.

D. rubiventris Borgmeier, 1935: 111. Holotype in Instituto Biologia Vegetal, Rio de Janeiro.

Distribution. Neotropical region: Brazil (*D. euxestae* and *D. rubiventris*; Weld, 1952). I have also seen undescribed species from southern Mexico, Costa Rica, Panama and Ecuador.

Biology. *Dettmeria euxestae* has been reared from the otitids *Euxesta eluta* Loew (Valicente, 1986) and *Euxesta* sp. (Borgmeier, 1935).

Remarks. This genus is deeply nested within Zaeucoilini, and sister to *Lopheucoila*. It shares many character states with *Lopheucoila* (including biology), leading to high branch support for the sister-group relationship. The lack of a distinct tooth overhanging the midpit of the scutellar plate is not only of diagnostic value, but is of phylogenetic importance as well, unequivocally separating this genus from *Lopheucoila*. Morphbank image collection: 228458.

Dicerataspis Ashmead

Dicerataspis Ashmead, 1895: 744. Type species: *Dicerataspis grenadensis* Ashmead, 1895: 744, by monotypy. Redescribed by Weld (1921).

Dissodontaspis Kieffer, 1909: 59. Type species: *Dissodontaspis flavipes* Kieffer, by monotypy. Synonymy by Weld (1952).

Diagnosis. Genal carina absent. Mesoscutal carina absent. Pronotal triangle small. Posterior projections of the mesoscutellum very long; lateral projections of the mesoscutellum reduced to absent. Most similar to *Preseucoela* in that both groups lack genal carinae, but *Preseucoela* lacks any projections off the posterior margin of the mesoscutellum.

Redescription

Head. Nearly glabrous with sparse setae along lower face, clypeus, gena and near ocelli. Ocellar hair patch absent. Ventral quarter of lower face with admedial clypeal furrows converging towards clypeus. Orbital furrows originating from lateral aspect of torulus, meeting malar sulcus at clypeal margin, resulting in the formation of a small triangular space between orbital furrow and malar sulcus. Malar sulcus simple. Malar space smooth with a few setae; protuberances absent. Genal carina absent.

Antenna. Female: 13 segments, moniliform, clavate; segments 3–6 one-half the length and width of segments 7–13; rhinaria present on segments 7–13. Male: 15 segments, moniliform; rhinaria present on segments 3–15; segments 4–15 subequal in length; segment 3 modified, slightly longer than segments 4–15, curved outwardly, excavated laterally.

No claims to original US government works

Pronotum. Pronotal plate medium sized, about one-half the width of the mesoscutum (viewed anterodorsally), with a few scattered setae along dorsal margin; dorsal margin rounded; pronotal fovea open. Pronotal triangle present. Pronotal impression absent. Lateral pronotal carina absent. Lateral aspect of pronotum (ventral to pronotal triangle) smooth and glabrous.

Mesoscutum. Smooth and glabrous; no sculpture present. Parascutal impression incomplete, narrow. Notauli, mesoscutal keel, parapsidal ridges and parapsidal hair lines absent.

Mesopectus. Upper part and lower part of mesopleuron smooth and glabrous. Dorsal margin of mesopleural triangle well defined, rounded ventrally. Mesopleural carina simple. Lower part of mesopleuron bounded by a distinct precoxal carina; surcoxal depression present, reticulate.

Mesoscutellum. Scutellar plate small; midpit placed posteriorly; rim of plate translucent; tubercles absent. Dorsal surface reticulate, margined laterally, rounded posteriorly. Laterodorsal projections present, reduced; posterior projections present, well developed. Lateral bars as long as wide, ventral lobe present. Scutellar fovea semicircular, smooth and deep.

Metapectal–propodeal complex. Metapectus mostly glabrous with a few long, scattered setae posteriorly. Spiracular groove shallow with a well-defined dorsal margin, reduced ventral margin. Posterior margin of metapectus ridged. Metapleural ridge absent; submetapleural ridge absent. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity subcircular, setose. Propodeum partially setose dorsally above the lateral propodeal carina; small patch of setae present at the ventral-most margin of the propodeum; remaining propodeal surface glabrous. Lateral propodeal carinae nearly parallel; auxiliary propodeal carinae reduced. Nucha glabrous, rugose.

Wings. Hyaline, with base of wing occasionally darkened; setose. R_1 complete, rarely pigmented along the anterior margin (appearing to be 'open'). Apical fringe long and continuous from anterior margin of wing to posteroventral corner.

Legs. Fore and mid coxa subequal in size, hind coxa twice the size of either fore or mid coxa. Fore coxa variably setose; mid coxa with an anterior dorsoventral setal band; hind coxa with setae scattered along lateral margin, dense setal patch present on posterior margin. Femora sparsely setose, tibiae slightly more setose, some setae appressed; tarsomeres covered in dense, appressed setae. Length of hind tarsomere 1 equal to one-half the combined length of remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, interrupted dorsally; setae dense, of all one length; remainder of metasoma smooth and glabrous. Micropunctures present on posterior third of syntergum, and on remaining terga. Terga posterior to syntergum abruptly angled ventrally, resulting in a 90° angle between the syntergum and remaining terga. Male: as in female.

Included species

**D. flavipes* (Kieffer), Weld (1952). *Dissodontaspis flavipes* Kieffer, 1909: 60. Holotype in CAS (#10534).

**D. grenadensis* Ashmead, 1895: 744. Holotype in USNM (#6506).

Distribution. Neotropical region: Caribbean, British West Indies (*D. grenadensis*; Dalla Torre & Kieffer, 1910) and Brazil (*D. flavipes*; Weld, 1952). I have seen undescribed species from Ecuador, Venezuela, Panama, Costa Rica, southern Mexico and the Caribbean.

Biology. The biology of *Dicerataspis* was comprehensively reviewed by Wharton *et al*. (1998). Species of *Dicerataspis* have been associated with the tephritid genera *Anastrepha* Schiner and *Rhagoletis* Loew (based on rearing records housed in the USNM), but Wharton *et al*. (1998) were unable to confirm these records. However, Wharton *et al*. (1998) recorded a *Dicerataspis* from a carefully isolated Drosophilidae puparium. Based on these data, Wharton *et al*. (1998) concluded that *Dicerataspis* is probably not a parasitoid of Tephritidae. However, Guimarães *et al*. (1999) did record *Dicerataspis* from *Anastrepha* Schiner infesting star fruit (*Averrhoa carambola* L.), although it is not clear whether puparia were isolated in this study.

Remarks. Many synapomorphies support the monophyly of this genus. The complete lack of a genal carina is shared only with species of *Preseucoela* and some *Agrostocynips*. The rounded dorsal margin of the pronotal plate is also unique within the Zaeucoilini, where a dorsally emarginate pronotal plate is more common. The narrow anteroventral inflection of the pronotum and the distinct separation between the anteroventral inflection and the pronotal plate are features common in the Diglyphosemini, but the possession of these states by *Dicerataspis* is unique within the limits of the Zaeucoilini. The complete lack of a mesoscutal keel is a reversal, independently derived in *Agrostocynips* and *Preseucoela*, and is constant across all species of *Dicerataspis*. The reduced size of the laterodorsal projections is a reversal, independent of the state found in *Marthiella*; this reduced state makes the posterior projections of the mesoscutellum to appear enlarged. The reduced impression of the mesopleural triangle is a reversal to the character state found frequently in the Diglyphosemini. The abruptly widened subalar area is an independent derivation relative to those Diglyphosemini that also possess this state. Morphbank image collection: 228629.

Lopheucoila Weld

Lopheucoila Weld, 1951: 223. Type species: *Diglyphosema anastrephae* Rohwer, 1919: 156, by original designation.

No claims to original US government works

Diagnosis. Posterior projections of mesoscutellum somewhat reduced, fused together medially. Base of syntergum of metasoma with distinct dorsoventral impressions. R_1 of wing not reaching the anterior margin of wing. Most similar to *Dettmeria* and *Penteucoila*, but easily separated from those groups by the dorsoventral impressions of the metasoma.

Redescription

Head. Nearly glabrous with a few scattered setae along lower face, clypeus and malar space. Ocellar hair patch present. Ventral quarter of lower face with admedial clypeal furrows converging towards the clypeus, somewhat reduced. Orbital furrows originating at lateral margin of the torulus and gently merging with malar sulcus ventrally. Malar sulcus simple. Malar space smooth; protuberances absent. Genal carina present from ventral margin of malar space to dorsal margin of compound eye; slightly flanged in parts posterior to compound eye.

Antenna. Female: 13 segments, subfiliform with segments before base moniliform; slightly clavate; segments 3–12 subequal in length, segment 13 1.5 times longer than segment 12; rhinaria present on segments 5–13. Male: 15 segments, moniliform; segments 3–15 subequal in length, with rhinaria; segment 3 modified, equal in length to segment 4, curved outwardly, excavated laterally.

Pronotum. Pronotal plate wide, with a few scattered setae along dorsal margin; dorsal margin crested, bifurcate; pronotal fovea open. Pronotal triangle present. Pronotal impression present. Lateral pronotal carina absent. Lateral part of pronotum (ventral to pronotal triangle) smooth and glabrous.

Mesoscutum. Mostly glabrous. Mesoscutal keel present, prominent anteriorly, occasionally reduced posteriorly. Parapsidal ridges present, reduced; parapsidal hair lines present. Parascutal impression incomplete, broad, with a distinct dorsal border appearing as a second pair of parapsidal ridges; aligned anteriorly with pronotal impression. Notauli absent.

Mesopectus. Upper part and lower part of mesopleuron glabrous, smooth. Dorsal and ventral borders of mesopleural triangle well defined. Mesopleural carina simple. Lower part of mesopleuron bounded by a reticulate precoxal carina; anterior and posterior surcoxal depressions deep, reticulate.

Mesoscutellum. Scutellar plate small; midpit placed midway between centre point of plate and posterior margin of plate; rim of plate translucent; prominent conical protuberance present anterior to midpit, slightly overhanging midpit. Dorsal surface reticulate, margined laterally and posteriorly. Laterodorsal projections knob-like; posterior projections reduced, fused medially, resulting in a straight posterior margin (when viewed dorsally). Lateral bars slightly longer than wide; ventral lobe present. Scutellar fovea large, nearly circular, smooth and deep.

Metapectal–propodeal complex. Anterior two-thirds of metapectus glabrous, variously setose on posterior third. Spiracular groove with well-defined dorsal and ventral margins. Posterior margin of metapectus with a prominent ridge. Metapleural ridge present, distinct; submetapleural ridge present, distinct, connecting the ventral margin of the spiracular groove to the metapleural ridge. Posteroventral portion of metapectus with several deep fovea. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity slit-like and setose; extending dorsally towards anterior impression of metepisternum. Propodeum covered in long, erect setae. Lateral propodeal carinae nonparallel, strongly bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae reduced. Nucha glabrous, slightly strigose.

Wings. Hyaline; glabrous. R_1 incomplete, not reaching anterior margin of wing; marginal cell slightly longer than deep; all wing veins lightly pigmented. Apical fringe absent.

Legs. Fore and mid coxa subequal in size, hind coxa 1.5 times the width of either fore or mid coxa. Fore coxa variously setose; mid coxa with anterior and lateral dorsoventral setal bands; hind coxa with lateral and posterior dorsoventral setal bands. Femora and tibiae sparsely setose; tarsomeres with dense appressed setae. Length of hind tarsomere 1 equal to two-thirds the combined length of remaining hind tarsomeres.

Metasoma. Female: conspicuously larger than mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, usually interrupted apically; remainder of metasoma glabrous. Lateral aspect of syntergum, posterior to setal band, with a strigose dorsoventral impression. Micropunctures present on posterior third of syntergum and on remaining terga. Terga posterior to syntergum gently angled ventrally, resulting in a 70° angle between syntergum and remaining terga. Male: as in female but with terga posterior to syntergum abruptly angled ventrally, resulting in a 90° angle between syntergum and remaining terga.

Included species

- **L. anastrephae* (Rohwer), Weld, 1951: 223. *Diglyphosema anastrephae* Rohwer, 1919: 156. Holotype in USNM (#22029).
- **L. mexicana* Weld, 1951: 224. Holotype in USNM (#60981).
- **L. truncicola* Weld, 1951: 223–224. Holotype in USNM (#60980).

Distribution. Neotropical region: Caribbean, British West Indies (*L. anastrepha*; Weld, 1952) southern Mexico (*L. mexicana*; Weld 1952) and Brazil (*L. trunicola*; Weld, 1952).

No claims to original US government works

Biology. Host associations for *Lopheucoila* have been recorded as *Anastrepha* (Rohwer, 1919) and *A. fraterculus* (Wiedemann) and species of *Lonchaea* Fallén (Weld, 1951). No host remains have ever been associated with these older records. Wharton *et al.* (1998) isolated and reared 69 012 puparia of *Anastrepha* and *Ceratitis* Macleay from a variety of fruits, and did not recover a single *Lopheucoila* species. However, Wharton *et al.* (1998) did recover 47 specimens of *Lopheucoila anastrepha* from the lonchaeid *Neosilba batesi* (Curran). Conversely, Guimarães (1998) reported *Lopheucoila anastrepha* as a parasitoid of three species of *Anastrepha*, namely *A. amita* Zucchi, *A. pseudoparallela* (Loew) and *A. fraterculus*, as well as a species of *Neosilba* McAlpine; it is not clear if puparia were isolated in the latter study.

Remarks. This genus is closely related to *Dettmeria*. Several distinctive synapomorphies support the monophyly of this group. The present but reduced state of the ocellar hair patch is unique within the core genera of the Zaeucoilini, and is lacking in some individuals of *L. anastrephae*. The lack of an apical fringe on the forewing, the R_1 vein of the forewing not meeting the anterior margin of the wing and the possession of dorsoventral linear impressions on the base of the syntergum of the metasoma are all unique features within the Zaeucoilini. Morphbank image collection: 228463.

Marthiella Buffington, **gen.n.**

Type species: *Rhabdeucoela flavotincta* Kieffer, 1908:46, by present designation.

Diagnosis. Orbital furrows originating either at lateral ocellus or lateral side of torulus. Genal carina well developed, flanged posterior to compound eye. Mesoscutal keel present. Parapsidal ridges absent. Parapsidal hair lines present. Laterodorsal projections of mesoscutellum present. R_1 never tubular or pigmented (radial cell 'open'). Superficially similar to *Tropideucoila* based on the presence of the parapsidal hair lines, which can look to the untrained eye like parapsidal ridges; easily separated from this genus by the lack of true parapsidal furrows, as well as a lack of posterior projections of mesoscutellum (only lateral projections present in *Marthiella*). Also similar to *Zaeucoila* and *Agrostocynips*, but differs from them by the presence of the extended orbital furrows (in some species), the presence of parapsidal hair lines and R_1 incomplete.

Description

Head. Nearly glabrous, with a few scattered setae along lower face, clypeus, inner orbits of compound eyes, malar space and gena. Ocellar hair patches present. Ventral quarter of lower face with admedial clypeal furrows converging towards clypeus. Orbital furrows present, originating at lateral side of ocellus, terminating at malar sulcus. Malar sulcus simple. Malar space smooth with a single prominent conical protuberance. Genal carina present, extending from malar space to lateral ocelli, frequently undulating posterior to compound eye.

Antenna. Female: 13 segments, moniliform, semiclavate; segments 3–13 subequal in length; rhinaria present on segments 3–13. Male: 15 segments, filiform; rhinaria present on segments 3–15; segments 4–15 subequal in length; segment 3 slightly longer than segment 4, curved outwardly, excavated laterally.

Pronotum. Pronotal plate wide, with setae along dorsal margin; slightly crested and bifurcate dorsally; pronotal fovea open. Pronotal triangle present (PT, Fig. 2C). Pronotal impression absent. Lateral pronotal carina absent. Lateral aspect of pronotum (below pronotal triangle) smooth and glabrous.

Mesoscutum. Smooth with some setae. Mesoscutal keel present, reaching posterior margin of mesoscutum; tapering posteriorly. Parapsidal ridges absent; parapsidal hair lines present (PHL, Fig. 2F). Parascutal impression incomplete, narrow. Notauli absent.

Mesopectus. Upper and lower parts of mesopleuron glabrous and smooth. Dorsal margin of mesopleural triangle well defined, rounded ventrally. Mesopleural carina simple. Lower part of mesopleuron bordered by distinct precoxal carina; anterior surcoxal depression present, reticulate.

Mesoscutellum. Scutellar plate ranging from medium to large; midpit placed centrally on plate; plate truncated posteriorly, always bearing tubercles and setae on dorsal surface. Dorsal surface reticulate; margined laterally and posteriorly. Laterodorsal projections present (LDP, Fig. 1F); posterior projections absent.

Metapectal–propodeal complex. Metapectus nearly glabrous with a few scattered setae posteriorly. Spiracular groove with a well-defined dorsal and ventral margin. Posterior margin of metapectus ridged. Metapleural ridge absent; submetapleural ridge present. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity semicircular and setose. Propodeum covered in long setae. Lateral propodeal carinae semiparallel, bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae indistinct. Nucha glabrous, reticulate.

Wings. Hyaline, with base of forewing frequently darkened; usually setose basally, always setose apically. R_1 incomplete, marginal cell as long as deep. Apical fringe present, short.

Legs. Fore and mid coxae about the same size, hind coxa about twice size of either fore or mid coxae. Fore coxa variably covered in long setae; mid coxa with anterior and posterior dorsoventral setal bands; hind coxa with a prominent setal band on hind margin. Femora and tibiae sparsely

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setose; tarsomeres with dense, appressed setae. Length of hind tarsomere 1 equal to 0.5 times combined length of remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, ranging from complete to dorsally bare, comprised of short, semi-appressed setae and longer erect setae; remainder of metasoma glabrous. Micropunctures present on posterior quarter of syntergum, and on remaining terga. Terga posterior to syntergum directed posteroventrally, resulting in a 70° angle between syntergum and remaining terga. Male: as in female but terga posterior to syntergum abruptly angled ventrally, resulting in a 90° angle between syntergum and remaining terga.

Included species

M. flavotincta* (Kieffer) **comb.n. *Rhabdeucoela flavotincta* Kieffer 1908: 46. Holotype in CAS (#10537). *Aegeseucoela flavotincta* (Kieffer): Buffington, 2002.

Distribution. Nearctic region: U.S.A.: AZ; Neotropical region: Mexico (Veracruz, Tamaulipas), Costa Rica, Panama, Belize (Buffington, 2002).

Biology. The only included species, *M. flavotincta* (Kieffer), was reared from the agromyzid flies *Haplopeodes* sp. on *Solanum erianthum* D. Don (Solanaceae) and *Calycomyza hyptidis* Spencer on *Hyptis capitata* Jacq. and *H. urticoides* Kunth (Lamiaceae) (O. Lewis, unpublished data; Buffington, 2002).

Etymology. This genus is named in honor of my mother Martha Buffington.

Remarks. The classification history of *Marthiella flavotincta* is indicative of the confusion surrounding this taxon. Fontal-Cazalla *et al.* (2002) erroneously coded *Tropideucoila* using this taxon, presumably based on the superficially similar parapsidal ridges of the mesoscutum and well-developed mesoscutal keel. Buffington (2002) rectified this, but the monophyly of *Aegeseucoela* (a new name proposed for both *A. flavotincta* and *A. grenadensis*) was not thoroughly tested until Buffington *et al.* (2007). *Marthiella flavotincta* is unique in that the orbital furrows of the head extend completely from the malar space to the lateral ocelli along the inner orbits of the eyes; the only other species of Zaeucoilini in which this character occurs is in *Penteucoila triloris*. Some *Rhabdeucoela* have orbital furrows extending to the ocelli, but this state always occurs with medially positioned orbital furrows. Morphbank image collection: 228796.

Moneucoela Kieffer

Moneucoela Kieffer, 1907: 90. Type species: *Moneucoela tinctipennis* Kieffer, 1907: 90, subsequent designation by Weld (1952).

Diagnosis. Orbital furrows curving gently to junction with malar sulci. Pronotal triangle present, small. Mesoscutal keel present. Parapsidal ridges and parapsidal hair lines absent. Laterodorsal and posterior projections of the mesoscutellum present. Anterior impression of metepisternum large. Superficially, members of this genus look like *Zaeucoila* due to the distinct mesoscutal keel. However, *Zaeucoila* lack laterodorsal and posterior scutellar projections.

Redescription

Head. Nearly glabrous with a few sparse setae along lower face, clypeus and gena. Ocellar hair patch absent. Lower face absolutely smooth; admedial clypeal furrows reduced. Orbital furrows originating at lateral margins of torulus and terminating at clypeus after gently curving to join malar sulcus. Malar sulcus compound to simple. Malar space smooth; ventral margin with a single conical protuberance. Genal carina extending from ventral margin of malar space to dorsal margin of the compound eye.

Antenna. Female: 13 segments, moniliform; segments 3–13 subequal in length; rhinaria present on segments 3–13. Male: 15 segments, moniliform; rhinaria present on segments 3–15; segments 3–15 subequal in length; segment 3 modified, slightly curved outwardly, excavated laterally.

Pronotum. Pronotal plate wide, with sparse setae along dorsal margin; crested dorsally, bifurcate; pronotal fovea open. Pronotal triangle present. Pronotal impression absent. Lateral pronotal carina absent. Lateral aspect of pronotum (ventral to pronotal triangle) smooth and glabrous.

Mesoscutum. Smooth and glabrous. Mesoscutal keel present, narrow, continuous to posterior margin of mesoscutum, tapering just after point of origin. Parascutal impression incomplete, broad and shallow. Notauli, parapsidal ridges and parapsidal hair lines absent.

Mesopectus. Upper part and lower part of the mesopleuron smooth and glabrous. Dorsal and ventral margins of mesopleural triangle well defined (at least anteriorly). Mesopleural carina simple. Lower part of mesopleuron bounded ventrally by a distinct precoxal carina; surcoxal depression prominent, reticulate.

Mesoscutellum. Scutellar plate small; midpit in centre of plate; rim of plate translucent; a single pair of small tubercles present anterior to midpit. Dorsal surface reticulate, margined laterally and posteriorly. Laterodorsal and posterior projections present. Lateral bars as long as wide; ventral lobe present. Scutellar fovea oval, smooth and deep.

Metapectal–propodeal complex. Metapectus glabrous with a few scattered setae. Spiracular groove with distinct dorsal and ventral margins. Posterior margin of metapectus ridged. Metapleural ridge absent; submetapleural ridge present from ventral margin of spiracular groove to a point

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corresponding to the anterior origin of metapleural ridge. Anterior impressions of metepimeron and metepisternum present; anterior impression of metepisternum very large. Anteroventral cavity oval, setose. Propodeum with scattered short and long setae, with a dense patch of setae on posterior aspect of metapectus. Lateral propodeal carinae subparallel, bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae indistinct. Nucha glabrous, smooth.

Wings. Hyaline; setose. R_1 complete, pigmented along anterior margin of wing; marginal cell as long as deep. Apical fringe present, long, especially along posterolateral curve of wing.

Legs. Fore and mid coxa subequal in size, hind coxa twice the size of either fore or mid coxa. Fore coxa variously setose; mid coxa with lateral and posterior setal patches; hind coxa with a thin lateral setal band and a dense posterior setal patch. Femora and tibiae sparsely setose; tarsomeres with dense, appressed setae. Length of hind tarsomere 1 equal to 0.75 times the combined length of remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, usually interrupted apically; composed of mostly short, dense setae; remainder of metasoma glabrous. Micropunctures present on posterior quarter of syntergum, and on remaining terga. Terga posterior to syntergum abruptly directed ventrally, resulting in a 90° angle between the syntergum and remaining terga. Male: as in female.

Included species

**M. parvicupula* Kieffer, 1907: 91. Holotype in CAS (#10583).
**M. tinctipennis* Kieffer, 1907: 90. Holotype in CAS (#10583).

Moneucoela sexdentata (Kieffer), Diaz & Gallardo, 1997. *Zaeucoila sexdentata* Kieffer, 1908: 46. Synonymy by Diaz & Gallardo (1998).

Distribution. Neotropical region: Belize (*M. parvicupula* and *M. tinctipennis*; Weld, 1952) and Nicaragua (*M. tinctipennis*; Kieffer, 1908). I have seen unidentified specimens from Mexico: Tamaulipas; Dominica: St. Paul Parish; Colombia: Choco; Ecuador: Napo.

Biology. I have examined a specimen of *Moneucoela parvicupula* taken on an unidentified dipteran host from an unidentified composite flower collected by Owen Lewis. Biology otherwise unknown.

Remarks. Although this genus is diagnosed readily from other genera of Zaeucoilini, only two autapomorphies support the monophyly of the genus. The exceptionally large anterior impression of the metepisternum is a striking feature, unlike any other genus in the Zaeucoilini. The complete R_1 vein along the anterior margin of the wing appears to be a reversal to the groundplan state; a unique feature with respect to the genera closely related to *Moneucoela*.

Weld (1952) uncovered the fact that Kieffer (1907) made *Moneucoela* available inadvertently, whereas the description of this 'new genus' was still in press (i.e. Dalla Torre & Kieffer, 1910). Weld (1952) did not mention the placement of *grenadensis* or *flavipes*, the two species described in *Moneucoela* Dalla Torre & Kieffer, 1910, essentially leaving them unplaced and *Moneucoela* Dalla Torre & Kieffer, 1910 a junior homonym that was not replaced. Buffington (2002) proposed the replacement name *Aegeseucoela* Buffington, transferring the species contained within *Moneucoela* Dalla Torre & Kieffer, 1910 to this genus and recognizing *Moneucoela* Dalla Torre & Kieffer, 1910 as a junior homonym of *Moneucoela* Kieffer, 1907. Morphbank image collection: 228350.

Moritiella Buffington

Moritiella Buffington, 2006: 62. Type species: *Moritiella elegans* Buffington, 2006: 66, by original designation.

Diagnosis. The following combination of characters separate *Moritiella* from the other previously described genera within the Zaeucoilini: orbital furrows entirely lacking. Genal carina present along ventral half to third of head. Conical projections absent on malar space. Pronotal plate broad; pronotal struts absent. Mesoscutum lacking any sculpture. Scutellar plate with two rows of posterodorsally oriented tubercles surrounding glandular release pit. Scutellar disk lacking projections. R_1 of forewing always tubular and pigmented; radial cell always closed.

Included species

**M. astrudae* Buffington, 2006: 67. Holotype in CNC.
**M. elegans* Buffington, 2006: 66. Holotype in CNC.

Distribution. Neotropical region: Colombia and Ecuador (*M. elegans* and *M. astrudae*); Dominica (*M. astrudae*); Venezuela and Brazil (*M. elegans*) (Buffington, 2006). Biology unknown.

Remarks. Some characters common to most Zaeucoilini are lacking in this genus, including orbital furrows and conical projections of the malar space. The most striking feature of this taxon are the well-developed posterodorsal directed tubercles surrounding the glandular release pit of the mesoscutellum. In lateral view, these tubercles appear like sawblade teeth. This taxon was found to be the sister group of *Zaeucoila*, and even though there are no host records available, the included species may also be parasitoids of Agromyzidae, like the majority of Zaeucoilini. Morphbank image collection: 228337.

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Penteucoila Weld

Penteucoila Weld, 1951: 225. Type species *Penteucoila triloris* Weld, 1951: 225, by original designation and monotypy.

Diagnosis. Orbital furrows present, originating at lateral ocellus. Ocellar hair patch present. Genal carina present. Parapsidal ridges and parapsidal hair lines present. Scutellar plate with a distinct protuberance overhanging midpit. Laterodorsal and posterior projections of the mesoscutellum present. Metasoma subequal in size to mesosoma. Most readily separated from *Lopheucoila* by the better developed posterior projections of the mesoscutellum, and the nearly equal sized meso- and metasomas; readily separated from *Tropideucoila* by the presence of the single protuberance on scutellar plate.

Redescription

Head. Nearly glabrous with a few scattered setae along lower face, clypeus and inner orbits of compound eyes. Ocellar hair patch present. Lower quarter of lower face with admedial clypeal furrows converging towards clypeus. Orbital furrows deep, originating from lateral ocellus and terminating at malar sulcus below compound eye. Malar sulcus simple. Malar space smooth; protuberances absent. Genal carina present, running from ventral margin of malar space to lateral ocelli.

Antenna. Female: 13 segments, moniliform, clavate; length of segments 3–6 equal to one-half each of the length of segments 7–12; segment 13 equal to twice the length of segment 12; rhinaria present on segments 7–13. Male: unknown.

Pronotum. Pronotal plate wide with dorsal margin sparsely setose; crested dorsally, bifurcate; pronotal fovea open. Pronotal triangle present. Pronotal impression present. Lateral pronotal carina absent. Lateral portion of pronotum (ventral to pronotal impression) smooth and glabrous.

Mesoscutum. Smooth and generally glabrous. Mesoscutal keel complete, tapering towards the middle and expanding slightly posteriorly. Parapsidal ridges present; parapsidal hair line present. Parascutal impression incomplete, broad, aligned anteriorly with pronotal impression. Notauli absent.

Mesopectus. Upper part and lower part of mesopleuron smooth and glabrous. Dorsal and ventral margins of mesopleural triangle distinct. Mesopleural carina simple. Lower part of mesopleuron bordered by a prominent precoxal carina; anterior and posterior surcoxal depressions present, reticulate.

Mesoscutellum. Scutellar plate small; midpit placed midway between centre of plate and posterior margin of plate; rim of plate translucent; prominent conical protuberance present in the centre of plate, overhanging midpit. Dorsal surface rugose; margined laterally and posteriorly; laterodorsal and posterior projections present. Lateral bars slightly longer than broad; ventral lobe present. Scutellar fovea large, semicircular, smooth and deep.

Metapectal–propodeal complex. Metapectus entirely glabrous. Spiracular groove with well-defined dorsal and ventral margins. Posterior margin of metapectus ridged. Metapleural ridge present, prominent; submetapleural ridge present, undulating. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity circular, setose. Propodeum covered in long, appressed setae. Lateral propodeal carinae semiparallel, bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae indistinct. Nucha glabrous, rugose.

Wings. Hyaline, with base of wing darkened; sparsely setose. R_1 incomplete; marginal cell slightly longer than deep. Apical fringe present, short.

Legs. Fore and mid coxa subequal in size, hind coxa twice the size of either fore or mid coxa. Fore coxa variously setose; mid and hind coxa with anterior and posterior dorsoventral setal bands. Femora and tibiae sparsely setose; tarsomeres covered with dense appressed setae. Length of hind tarsomere 1 equal to 0.5 times the combined length of remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, interrupted apically, composed of both short and long setae; remainder of metasoma glabrous. Micropunctures present on posterior half of syntergum and on remaining terga. Terga posterior to syntergum abruptly directed ventrally, resulting in a 90° angle between syntergum and remaining terga. Male: unknown.

Included species

**P. triloris* Weld, 1951: 225. Holotype in USNM (#60982), paratypes in NHM.

Distribution. Neotropical: Mexico, Trinidad and Guyana (Weld, 1952). Biology unknown.

Remarks. This genus is closely related to *Tropideucoila*. Although the genus is readily diagnosed from other Zaeucoilini, only two rather weak synapomorphies support the monophyly of the genus. The orbital furrows originating at the lateral ocelli are also shared with *Marthiella* and *Rhabdeucoela*; this feature was probably independently gained in all three genera. The distinctly protruding anterior flange of the pronotal plate appears to be a reliable character, especially as it is visible in museum specimens. In most other Eucoilinae, this feature is only visible when the head has been removed from the mesosoma; more specimens of this genus need to be examined to clarify the status of this character state. Additionally, this feature is shared with *Rhabdeucoela* through parallel gain. Morphbank image collection: 228459.

No claims to original US government works

Preseucoela Buffington

Preseucoela Buffington, 2004: 2. Type species *Preseucoela imallshookupis* Buffington, 2004: 6–7, by original designation.

Diagnosis. Orbital furrows meeting malar sulcus with smooth curve. Genal carina absent. Conical projections present on malar space. Pronotal struts present between posterior margin of pronotal plate and anterior margin of mesoscutum. Mesoscutal keel present or absent. Scutellar plate with two distinct tubercles. Scutellar disk lacking projections. R_1 of forewing always tubular and pigmented; radial cell always closed. Differs from *Moneucoela* Kieffer by lacking lateral and posterior projections of mesoscutellum. Differs from *Zaeucoila* Ashmead and *Agrostocynips* Diaz by lacking genal carinae (reduced but distinct in *Agrostocynips*), and presence of paired tubercles on dorsal surface of scutellar plate (*Zaeucoila* and *Agrostocynips* have multiple tubercles). Differs from *Ganaspidium* Weld by presence of orbital furrows, presence of pronotal struts and possession of a large pronotal plate (pronotal plate in *Ganaspidium* one-third to one-quarter as wide as head).

Included species

**P. heratyi* Buffington, 2004: 6. Holotype in AEI.
**P. imallshookupis* Buffington, 2004: 6–7. Holotype in AEI.
**P. pallidipes* (Ashmead), Buffington (2004). *Chrestosema pallidipes* Ashmead, 1894: 68–69. Holotype in USNM (#2337).

Eucoila sancti-marci Kieffer 1908: 59. Synonymy by Buffington (2004).
Eucoila transversa Kieffer 1908: 59. Synonymy by Buffington (2004).
Pseudeucoila (*Heptamerocera*) *transversa* (Kieffer) Weld 1952: 239.

Distribution. Nearctic region: U.S.A.: Arizona, New Mexico (*P. heratyi*, *P. pallidipes*); Neotropical region: Caribbean (*P. heratyi*, *P. imallshookupis*, *P. pallidipes*); Costa Rica, Guatemala, Mexico (*P. imallshookupis, P. pallidipes*); Honduras (*P. imallshookupis*, *P. heratyi*), Bolivia, Ecuador, Venezuela (*P. heratyi*, *P. pallidipes*); El Salvador, Panama, Nicaragua, (*P. heratyi*), Colombia, Argentina (*P. pallidipes*).

Biology. Circumstantial and phylogenetic evidence suggests that members of *Preseucoela* are parasitoids of Agromyzidae; see Buffington (2004) for a detailed account of host associations that unfortunately lack host remains.

Remarks. Members of this genus typically resemble *Ganaspidium*, and often one can find specimens of *Preseucoela* in collections identified as *Ganaspidium*. *Preseucoela* is easily distinguished from *Ganaspidium* by the possession of a broad pronotal plate (like all other Zaeucoilini). Within Zaeucoilini, *Preseucoela* shares a number of characters with *Dicerataspis*, including the lack of a genal carina and the presence of simple yet distinct pronotal struts. The phylogenetic placement of *Preseucoela* is somewhat unstable. The Bayesian topology, finding *Preseucoela* as a sister group to the core Zaeucoilini (*Moneucoela* through *Dettmeria*; Fig. 5B), makes intuitive sense in the form of external morphology; the parsimony placement as a sister group to the remaining Zaeucoilini is much harder to justify, given that there are several character states shared with more derived Zaeucoilini (pronotal struts present, well-developed orbital furrows, presence of mesoscutal keel in *P. imallashookupis*). Morphbank image collection: 270851.

Rhabdeucoela Kieffer

Rhabdeucoela Kieffer, 1907: 70. Type species: *Rhabdeucoela nitidifrons* Kieffer, 1907: 71, by original designation.
Frireniella Kieffer, 1909: 64. Type species: *Frireniella bisulcata* Kieffer, 1909: 64–65, by monotypy. Synonymy by Weld (1952).

Diagnosis. Orbital furrows removed from inner orbits of compound eyes; instead, located more medially on ventral portion of lower face. Orbital furrow originating at lateral ocellus. Genal space dimpled. Pronotal impression present, angled dorsally. Mesoscutal keel broad, tapering posteriorly. Scutellar plate large, with small fovea present along rim. Mesoscutellum meeting underside of scutellar plate at a 90° angle. Spiracular groove exceptionally large, nearly tubular. A distinct protuberance present at fusion point of lateral propodeal carina and auxiliary propodeal carina.

Redescription

Head. Nearly glabrous with a few setae along lower face, clypeus, malar space, near ocelli and gena. Ocellar hair patch present. Cuticle dimpled between posterior margin of compound eye and genal carina (genal space). Admedial clypeal furrows on lower face joined with orbital furrows; the two furrows joining at anterior tentorial pits. Orbital furrows displaced medially on to lower face; originating from lateral ocellus; occasionally rugose. Malar sulcus simple to compound. Malar space glabrous, occasionally punctate; protuberances absent. Genal carina present, running from malar space to dorsal margin of compound eye; usually ridged.

Antenna. Female: 13 segments, moniliform, clavate; segments 3–13 subequal in length; rhinaria present on segments 3–13. Male: 15 segments; segments 4–15 subequal in length; rhinaria present on segments 3–15; segment 3 modified, slightly larger than segment 4, curved outwardly, excavated laterally.

Pronotum. Pronotal plate large, with sparse setae along dorsal margin; trapezoidal in shape when viewed anteriorly; sharply rounded dorsally, not crested; pronotal fovea open.

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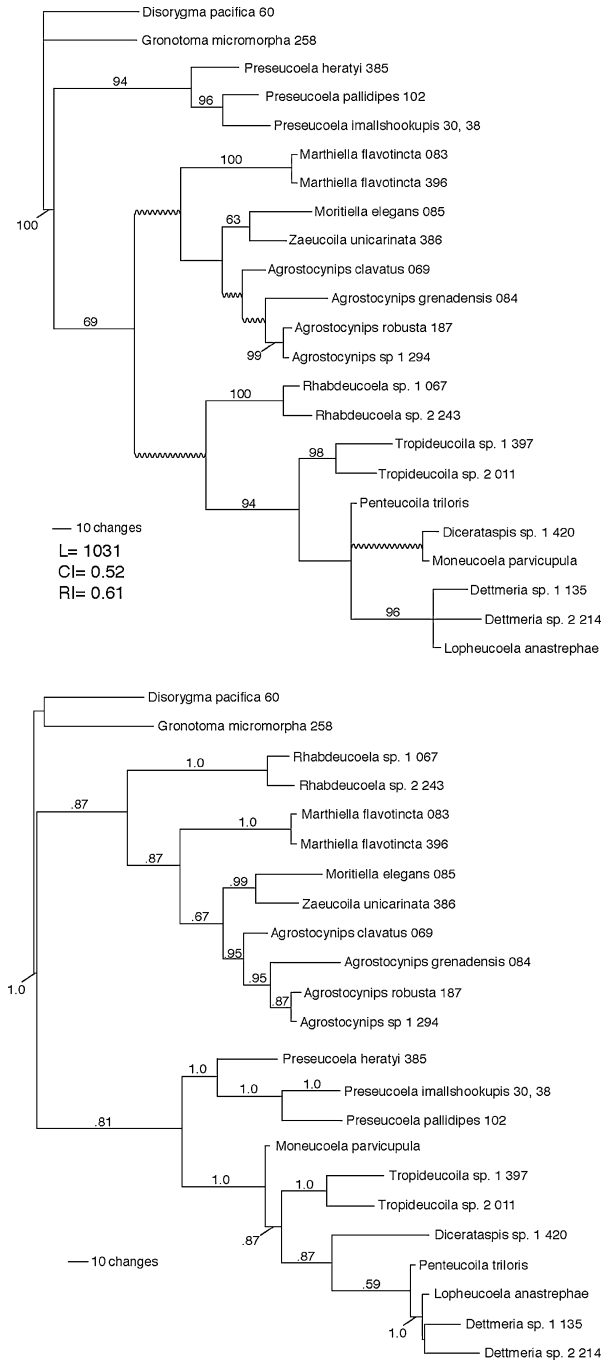

Fig. 5. Phylograms of Zaeucoilini. Total evidence (molecular and morphological datasets) based on parsimony followed by successive approximation weighting (A) and Bayesian inference (B). The numbers on the branches of (A) correspond to bootstrap support values (<50% not shown); zig-zag branches represent branches that collapse under strict consensus of equal weights parsimony; L = tree length, CI = consistency index, RI = retention index. The numbers on the branches of (B) correspond to posterior probabilities of clade recovery. The numbers after terminal names correspond to specimens listed in Supporting Information SI1.

Pronotal triangle absent. Pronotal impression present, directed mesally towards mesoscutum. Lateral pronotal carina absent. Lateral portion of pronotum (ventral to pronotal impression) smooth and glabrous.

Mesoscutum. Smooth and generally glabrous. Mesoscutal keel prominent anteriorly, reduced posteriorly; tapering posteriorly. Parascutal impression incomplete. Notauli, parapsidal ridges and parapsidal hair lines absent.

Mesopectus. Upper portion and lower portion of mesopleuron glabrous; lower portion occasionally dimpled. Dorsal and ventral margins of mesopleural triangle well defined. Mesopleural carina simple. Lower portion of mesopleuron bordered by a distinct precoxal carina; anterior and posterior surcoxal depressions present, small, reticulate.

Mesoscutellum. Scutellar plate large, midpit placed in centre; rim of plate translucent; surface surrounding midpit foveate; tubercles absent. Dorsal surface rugose, slightly overhanging propodeum; rounded and margined laterally and posteriorly; laterodorsal and posterior projections absent; meeting underside of scutellar plate at a 90° angle. Lateral bars as long as wide; ventral lobe absent. Scutellar fovea oval, smooth and deep.

Metapectal–propodeal complex. Metapectus glabrous except for a few long hairs along posterior margin and a small patch of setae within spiracular groove. Spiracular groove with massive dorsal and ventral borders. Posterior margin of metapectus ridged. Metapleural ridge absent; submetapleural ridge present. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity oval, setose. Propodeum with dense, appressed setae. Lateral propodeal carinae semiparallel, bowed at junction with auxiliary propodeal carinae; junctions marked with a prominent conical protuberance; auxiliary propodeal carinae indistinct. Nucha glabrous, reticulate.

Wings. Hyaline; setose. R_1 complete, pigmented along anterior margin of wing; marginal cell elongate, nearly twice as long as deep. Apical fringe present, short.

Legs. Fore and mid coxa subequal in size, hind coxa about twice the size of either fore or mid coxa. Fore coxa variously setose; mid coxa with faint anterior and posterior dorsoventral setal bands; hind coxa with a sparse lateral band of setae and a dense posterior patch. Femora and tibiae sparsely setose; tarsomeres with dense appressed setae. Length of hind tarsomere 1 equal to 0.75 times the combined length of remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring visible in some species. Base of syntergum with hairy ring present, composed of both short and long setae; remainder of metasoma glabrous. Micropunctures present on posterior quarter of the syntergum as well as on remaining terga. Terga posterior to syntergum angled

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posteroventrally, resulting in a 70° angle between syntergum and remaining terga. Male: as in female with terga posterior to syntergum abruptly directed ventrally at 90° relative to syntergum.

Included species

R. bidentata Kieffer, 1909: 92–93. Holotype in ZMNH.
**R. bisulcata* (Kieffer), Weld, 1952. *Frireniella bisulcata* Kieffer, 1909: 64–65. Holotype in CAS (#10507).
R. flavipes* (Ashmead) **comb.n.

Diglyphosema flavipes Ashmead, 1894: 61. Holotype in USNM.

Diranchis flavipes Ashmead, 1900: 248. Holotype in NHM. **Syn.n.**

**R. nitidifrons* Kieffer, 1907: 71. Holotype and syntype in CAS (#10577).
**R. opacifrons* Kieffer, 1907: 71. Holotype in CAS (#10580).
**R. semirufa* Kieffer, 1907: 71. Holotype in CAS (#10605).
**R. spatulifera* Kieffer, 1907: 90. Holotype in CAS (#10609).

Distribution. Neotropical region: Brazil (*R. bisulcata*); Belize (*R. nitidifrons*, *R. opacifrons*, *R. semirufa*); Nicaragua (*R. spatulifera*); Ecuador: Napo, Pich.; Bolivia: Santa Cruz (*R. bidentata*). I have seen unidentified specimens from Mexico: Tamaulipas, Veracruz; Panama: Colon; Dominica; Venezuela: Merida; Peru: Yahuarmayo; Colombia: Valle.

Biology. I have examined species of *Rhabdeucoela* reared by D. Havaranet from an unidentified species of *Melanagromyza* as well as an unidentified specimen reared by J. Etienne from *Melanagromyza* nr. *caerulea* (Malloch). These constitute the first rearing records of this genus.

Comments. The medially positioned orbital furrows, the pronotal impression running to a point mesal of the parascutal impression and the conical protuberances at the junction of the lateral propodeal carina with auxiliary carina on the propodeum, the exposed crenulate ring of the metasoma, and the mesoscutellum meeting the scutellar plate at a 90° angle are all unique features within the Zaeucoilini; apparently, this last feature motivated Ashmead (1894) to describe a species of *Rhabdeucoela* (*R. flavipes*) in *Diglyphosema* (see above). Other unique (but homoplastic) characters of this genus include the presence of orbital furrows extending from near the malar sulcus and continuing to the lateral ocellus; this is homoplastic in that this state is shared with *Marthiella* and *Penteucoila*. The presence of ocellar hair patches is also somewhat homoplastic, either independently gained by *Rhabdeucoela* and some of the other Zaeucoilini or a groundplan state for Zaeucoilini, secondarily lost by some members. The presence of distinct dorsal and ventral borders of the mesopleural triangle is homoplastic considering *Tropideucoila*, *Penteucoila*, *Moneucoela*, *Lopheucoila*, *Dettmeria* similarly possess this feature.

The phylogenetic placement of *Rhabdeucoela* within Zaeucoilini is rather unstable (Fig. 5). Parsimony recovers the clade as a sister group to (*Moneucoela*, *Penteucoila*, *Tropideucoila*, *Dettmeria*, *Lopheucoila*), whereas Bayesian inference suggests a sister grouping of the clade containing *Agrostocynips*, *Marthiella*, *Zaeucoila* and *Moritiella*. This latter grouping is supported by a moderately strong posterior probability, whereas the parsimony support value is less than 50% bootstrap; furthermore, this grouping collapses in the strict consensus of the unweighted tree. Hence, the parsimony result is far from robust.

Based on the examination of the holotype of *Diranchis flavipes* Ashmead, 1900, this species is hereby transferred to *Rhabdeucoela*, where it is both a junior subjective synonym of *flavipes* (Ashmead, 1894), as well as a junior, secondary homonym. Morphbank image collection: 228461.

Tropideucoila Ashmead

Tropideucoila Ashmead, 1903a: 221. Type species: *Tropideucoila rufipes* Ashmead, 1903a: 221, by original designation. Redescribed by Weld (1921).

Tropideucoela Ashmead, 1903b: 61. Unjustified emendation.

Trisseucoela Kieffer, 1907: 91. Type species: *Trisseucoela fulvotincta* Kieffer, 1907: 91, subsequent designation by Rohwer & Fagan (1917: 377). Synonymy by Weld (1952).

Diagnosis. Orbital furrows present, originating at torulus. Mesoscutal keel present, well developed. Parapsidal ridges and parapsidal hair lines present. Scutellar plate medium in size, often with two tubercles bearing setae anterior to the midpit; no large conical projection present on plate. R_1 vein of wing incomplete.

Redescription

Head. Nearly glabrous with a few scattered setae along lower face, clypeus and inner orbits of compound eyes. Ocellar hair patch present. Ventral quarter of lower face with admedial clypeal furrows converging towards clypeus. Orbital furrows originating from lateral aspect of torulus and terminating at malar sulcus. Malar sulcus simple. Malar space smooth to strigose; protuberances absent. Genal carina running from malar space to dorsal margin of compound eye.

Antenna. Female: 13 segments, moniliform, clavate to partially clavate; segments 6–13 wider than segments 3–5; segments 3–13 subequal in length; rhinaria present on segments 6–13. Male: 15 segments, moniliform; rhinaria present on segments 3–15; segments 4–15 subequal in length; segment 3 modified, slightly longer than segment 4, curved outwardly, excavated laterally.

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Pronotum. Pronotal plate wide, with sparse setae along dorsal margin; dorsal margin crested, bifurcate; pronotal fovea open. Pronotal triangle present. Pronotal impression present. Lateral pronotal carina absent. Lateral part of pronotum (ventral to pronotal impression) smooth and glabrous.

Mesoscutum. Distinctly sculptured and setose. Mesoscutal keel complete, tapering towards middle. Parapsidal ridges present; parapsidal hair lines present. Parascutal impression broad, aligned anteriorly with pronotal impression. Notauli absent.

Mesopectus. Upper part and lower part of mesopleuron glabrous, smooth. Dorsal and ventral margins of mesopleural triangle distinct. Mesopleural carina simple. Lower part of mesopleuron bordered by a prominent precoxal carina; anterior and posterior surcoxal depressions present, reticulate.

Mesoscutellum. Scutellar plate small to medium in size; midpit placed near posterior rim; rim of plate translucent; small paired tubercles often present anterior to the midpit. Dorsal surface rugose, margined laterally and posteriorly; laterodorsal and posterior projections present. Lateral bars slightly longer than broad; ventral lobe present. Scutellar fovea large, semicircular, smooth and deep.

Metapectal–propodeal complex. Metapectus entirely glabrous. Spiracular groove deep with well-defined dorsal and ventral margins. Posterior margin of metapectus ridged. Metapleural ridge prominent; submetapleural ridge undulating. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity circular, setose. Propodeum covered in long, appressed setae. Lateral propodeal carinae semiparallel, bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae indistinct. Nucha glabrous, rugose.

Wings. Hyaline, with base of wing often darkened; sparsely to entirely setose. R_1 incomplete; marginal cell slightly longer than deep. Apical fringe present, short.

Legs. Fore and mid coxa subequal in size, hind coxa twice the size of either fore or mid coxa. Fore coxa variously setose; mid and hind coxa with anterior and posterior dorsoventral setal bands. Femora and tibiae sparsely setose, tibiae with more appressed setae; tarsomeres covered in dense appressed setae. Length of hind tarsomere 1 equal to 0.5 times the combined length of remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, usually interrupted apically; composed of both short and long setae; remainder of metasoma glabrous. Micropunctures present on posterior half of syntergum and on remaining terga. Terga posterior to syntergum abruptly directed ventrally, resulting in a 90° angle between syntergum and remaining terga. Male: as in female.

Included species

T. angrensis Borgmeier, 1935: 110. Holotype in Instituto Biologia Vegetal, Rio de Janeiro (#7874).

T. atricornis (Kieffer), Weld, 1952: 196. *Trisseucoela atricornis* Kieffer, 1911: 121. Holotype in ZMHB.

**T. clavicornis* (Kieffer), Weld, 1952: 196. *Trisseucoela clavicornis* Kieffer, 1908: 45. Holotype in CAS (#10521).

**T. fulvonotata* (Kieffer), Weld, 1952: 196. *Rhabdeucoela fulvonotata* Kieffer, 1907: 90. Syntypes in CAS (one #10540).

**T. fulvotincta* (Kieffer), Weld, 1952: 196. *Trisseucoela fulvotincta* Kieffer, 1907: 91. Holotype in CAS (#10541).

**T. nigricornis* (Kieffer), Weld, 1952: 196. *Trisseucoela nigricornis* Kieffer, 1907: 91. Holotype in CAS (#10571).

**T. ruficornis* (Kieffer), Weld, 1952: 196. *Trisseucoela ruficornis* Kieffer, 1907: 91. Holotype in CAS (#10594).

**T. rufipedata* Weld, 1952: 196. Replacement name for *Trisseucoela rufipes* Kieffer, 1908: 45–46; preoccupied by *Tropideucoila rufipes* Ashmead. Holotype in CAS (#10596).

**T. rufipes* Ashmead, 1903a: 221. Holotype in USNM (#23648).

T. weldi Costa Lima, 1940: 17–18. Holotype in Instituto Oswaldo Cruz, Rio de Janeiro.

Distribution. Neotropical region: Brazil: Rondonia (*T. angrensis*); Nicaragua (*T. clavicornis*, *T. fulvonotata*, *T. nigricornis*, *T. ruficornis*, *T. rufipedata*); Belize (*T. fulvonotata*, *T. fulvotincta*). I have also seen unidentified species from Panama, Colombia, Ecuador, Venezuela and Argentina.

Biology. Species of *Tropideucoila* have been reared from *Liriomyza* (Acosta & Cave, 1994; determination by Göran Nordlander). I have also examined specimens of *Tropideucoila* reared from several species of *Calycomyza*, *Japanagromyza* and two unidentified agromyzids (O. Lewis, personal communication).

Remarks. This genus is closely related to *Penteucoila*, and is nested deep within the Zaeucoilini. Several synapomorphies support the monophyly of this genus. In approximately 90% of the species examined here, a single pair of tubercles are present anterior to the midpit of the scutellar plate (reduced in the remaining approximately 10%); this feature is also shared with *Moneucoela* and *Preseucoela*. Apart from having the tubercles mentioned previously, the generally flat area anterior to the midpit is unique within this part of the Zaeucoilini. Other genera tend to possess either a mound-like or conical protuberance in this area. The carina separating the two halves of the scutellar fovea is a unique feature within the *Zaeucoila* group, in this case long and extending on to the disk of the mesoscutellum (in other genera, the carina does not extend on to the disk of the mesoscutellum). The concave surface of the scutellar plate is also unique within the Zaeucoilini, where the

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trend is to have either a flat surface (e.g. *Dettmeria*) or a convex surface (e.g. *Diceratastpis*). It should also be noted that the size of the scutellar plate may be correlated with the concavity of the scutellar plate (i.e. smaller scutellar plates have a smaller degree of concavity); the scutellar plate of *Tropideucoila* is somewhat smaller than other Zaeucoilini, but is still larger than either *Dettmeria* or *Diceratastpis*. One very important feature is the fact that members of this genus are parasitoids of Agromyzidae; this feature is unique within this subclade of the Zaeucoilini, where the shift to Tephritidae (and allies) has taken place (*Dettmeria*, *Lopheucoila* and *Diceratastpis*); yet, definitive host records for *Moneucoela* and *Penteucoila* are required to fully determine the validity of this synapomorphy. If *Moneucoela* and *Penteucoila* are found to be parasitoids of Agromyzidae, then possession of this feature by *Tropideucoila* will be a symplesiomorphy. Morphbank image collection: 228462.

Zaeucoila Ashmead

Zaeucoila Ashmead, 1903a: 222. Type species: *Zaeucoila unicarinata* Ashmead, 1903a: 222, by original designation. Redescribed by Weld (1921).

Zaeucoela Ashmead, 1903b: 66, 71. Unjustified emendation.

Diagnosis. Genal carina present, running from ventral margin of malar space to near posterior margin of lateral ocellus. Orbital furrows present, weakly developed. Mesoscutal keel present, at least anteriorly. Scutellar plate usually with tubercles on dorsal surface. Midpit of scutellar plate positioned posteriorly. The members of this genus form a grade into *Agrostocynips*, which arguably can be considered as 'reduced' *Zaeucoila* species; as defined here, the two genera can be separated by the presence (*Zaeucoila*) or absence (*Agrostocynips*) of the mesoscutal keel, and the length of the genal carina (long in *Zaeucoila*, short in *Agrostocynips*) and the position of the midpit of the mesoscutellum (posteriorly located in *Zaeucoila*, centrally located in *Agrostocynips*).

Redescription

Head. Nearly glabrous with a few scattered setae along lower face, clypeus, inner orbits of compound eyes, malar space and gena. Ocellar hair patch absent. Ventral quarter of lower face with admedial clypeal furrows converging towards clypeus. Orbital furrows shallow, originating at torulus, terminating at malar sulcus. Malar sulcus simple. Malar space smooth; ventral margin with a single prominent conical protuberance. Genal carina running from malar space to dorsal margin of compound eye.

Antenna. Female: 13 segments, moniliform, semiclavate; segments 3–13 subequal in length; rhinaria present on segments 4–13. Male: 15 segmented, moniliform; rhinaria present on segments 3–15; segments 4–15 subequal in length; segment 3 slightly longer than segment 4, curved outwardly, excavated laterally.

Pronotum. Pronotal plate wide, with setae along dorsal margin; dorsal margin slightly emarginate; pronotal fovea open. Pronotal triangle absent. Lateral pronotal carina absent. Pronotal impression absent. Lateral aspect of pronotum glabrous and smooth.

Mesoscutum. Smooth and glabrous. Mesoscutal keel present, at least anteriorly, tapering towards posterior margin of mesoscutum. Parascutal impression incomplete, narrow. Notauli, parapsidal ridges and parapsidal hair lines absent.

Mesopectus. Upper part and lower part of mesopleuron smooth and glabrous. Dorsal margin of mesopleural triangle distinct, ventral margin rounded. Mesopleural carina simple. Lower part of mesopleuron bordered by a prominent precoxal carina; anterior surcoxal depression prominent, reticulate.

Mesoscutellum. Scutellar plate ranging from medium to large; midpit placed midway between centremost point of plate and hind margin; rim of plate translucent; prominent tubercles nearly always present along dorsal surface of rim. Dorsal surface reticulate, rounded and margined laterally and posteriorly; laterodorsal and posterior projections of mesoscutellum absent. Lateral bars as long as wide; ventral lobe present. Scutellar fovea oval, smooth and deep.

Metapectal–propodeal complex. Anterior two-thirds glabrous, posterior third setose. Spiracular groove with a distinct dorsal margin, ventral margin reduced. Posterior margin of metapectus ridged. Metapleural ridge present, reduced; submetapleural ridge absent. Anterior impressions of metepimeron and metepisternum present. Anteroventral cavity semicircular and setose. Propodeum covered in long setae. Lateral propodeal carinae semiparallel, bowed at junction with auxiliary propodeal carinae; auxiliary propodeal carinae indistinct. Nucha glabrous, reticulate.

Wings. Hyaline, base of wing sometimes darkened; setose. R_1 complete, pigmented along anterior margin of wing; marginal cell as long as deep. Setal fringe present, short.

Legs. Fore and mid coxa about subequal in size, hind coxa about twice the size of either the fore or mid coxa. Fore coxa variably setose; mid and hind coxa with anterior and posterior dorsoventral setal bands. Femora and tibiae sparsely setose; tarsomeres with dense, appressed setae. Length of hind tarsomere 1 equal to 0.85 times the combined length of the remaining hind tarsomeres.

Metasoma. Female: subequal in size to mesosoma. Crenulate ring not visible. Base of syntergum with hairy ring present, comprised of short, semi-appressed setae and longer erect setae. Micropunctures present on posterior quarter of syntergum, and on remaining terga. Terga posterior to syntergum directed posteroventrally, resulting

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in a 70° angle between syntergum and remaining terga. Male: as in female with terga posterior to syntergum abruptly angled ventrally, resulting in a 90° angle between syntergum and remaining terga.

Included species

**Z. incompleta* (Kieffer), Weld, 1952: 193. *Rhabdeucoela incompleta* Kieffer, 1907: 90, holotype in CAS (#10551).
**Z. triangulifera* Kieffer, 1907: 91, holotype in CAS (#10615).
**Z. unicarinata* Ashmead, 1903a: 222, holotype in USNM (#23650).

Distribution. Neotropical region: Caribbean Islands (*Z. incompleta*); Nicaragua (*Z. triangulifera*); Brazil (*Z. unicarinata*). I have also seen unidentified species from Argentina, Colombia, Ecuador, Dominica, Panama, Venezuela and Mexico.

Biology. *Zaeucoila* sp. has been reared from *Liriomyza sativae* Blanchard (Acosta & Cave, 1994). I have examined *Z. triangulifera* Kieffer from *Liriomyza* sp. infesting *Lactuca sativa* L., from *Amauromyza maculosa* (Malloch) and from *Agromyza fusca* Spencer; *Z. incompleta* (Kieffer) from *Nemorimyza maculosa* (Malloch); *Zaeucoila* **sp.n.** from *Liriomyza sativae*, from *Liriomyza marginalis* (Malloch) and *Calycomyza triumfette* Etienne (specimens from G. Delvar).

Remarks. This genus is closely related to both *Agrostocynips* and *Marthiella* (as discussed above). Only one putative synapomorphy supports the monophyly of this genus, i.e. the posterior position of the midpit of the scutellar plate. In both *Agrostocynips* and *Marthiella*, the trend is to have the midpit positioned towards the centre of the scutellar plate; a more posterior placement is also found in *Tropideucoila*, *Penteucoila*, *Diceratastpis*, *Moneucoela*, *Dettmeria* and *Lopheucoila*. The more parsimonious solution would be for a reversal to the centrally positioned midpit in *Marthiella* (one step), which results in this feature not being a synapomorphy of *Zaeucoila*, but one of the 'core' Zaeucoilini genera. Morphbank image collection: 228460.

Discussion

Phylogenetic patterns

The parsimony and Bayesian hypotheses of relationships suggest two different evolutionary histories within Zaeucoilini (Fig. 5), and in both cases, the taxa of interest are *Preseucoela* and *Rhabdeucoela*. In the parsimony scenario, *Preseucoela* was recovered as its own clade and sister group to the remaining Zaeucoilini. From a morphological standpoint, this pattern suggests that typical Zaeucoilini features, such as the presence of the genal carina and sculpturing on the mesoscutum (e.g. the mesoscutal keel and parapsidal ridges), are derived (as species of *Preseucoela* are devoid of these characters). The Bayesian hypothesis groups *Preseucoela* with the 'core' zeucoilines (*Moneucoela*, *Tropideucoila*, *Diceratastpis*, *Penteucoila*, *Lopheucoela* and *Dettmeria*), and *Rhabdeucoela* with another clade of zaeucoilines (*Marthiella*, *Agrostocynips*, *Moritiella* and *Zaeucoila*). From a morphological standpoint, the Bayesian result is more intuitive; the presence of the pronotal struts and the morphology of the scutellar plate are very similar in *Preseucoela* to *Moneucoela* and *Diceratastpis*. The phylogenetic uncertainty of *Rhabdeucoela* is also intriguing; this taxon abounds with autapomorphies (see above), but not many characters that unequivocally link it to another clade. The well-developed keel is a character shared with several 'core' zaeucoilines, although this same character is present in *Marthiella* and some *Zaeucoila*. The remaining Zaeucoilini are recovered consistently the same regardless of the phylogenetic method.

Distribution patterns

The Zaeucoilini, as a whole, is restricted almost entirely to the Neotropics. Buffington & Scheffer (2008) examined specimens of *Agrostocynips robusta* and *A. diastrophi* collected from Argentina and Brazil, through Central America, and all the way up to upstate New York, U.S.A. It is unknown why this particular genus is capable of such an incredibly broad range, when other closely related taxa (e.g. *Zaeucoila*) show no such patterns. *Marthiella* has also been collected in the southern Nearctic region, but this genus is much less widespread than *Agrostocynips*. The northern limit of the remaining genera of Zaeucoilini appears to be southern Mexico (Oaxaca and Chiapas); the southern distribution limits and altitudinal limits of the genera in this tribe remain to be examined.

Supporting Information

Additional Supporting Information may be found in the online version of this article from Wiley Interscience under DOI reference: doi: 10.1111/j.1365-3113.2008.00447.x

SI1 List of included Zaeucoilini, GenBank accessions.
SI2 Description of morphological characters.
SI3 Phylogeny supporting outgroup choice.

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Acknowledgements

I sincerely appreciate Robert Wharton, James Woolley and John McEachran (Texas A&M University, College Station,

TX, U.S.A.) for their guidance in the pursuit of this project. Additional thanks to Göran Nordlander (Swedish Agricultural University, Uppsala, Sweden) and Fredrik Ronquist (Swedish Museum of Natural History, Stockholm, Sweden) for outstanding guidance and support throughout this project. Special thanks to John LaSalle (CSIRO, Canberra, Australia), Owen Lewis (University of Oxford, U.K.) and Sonja Scheffer (Systematic Entomology Laboratory, Beltsville, MD, U.S.A.) for providing reared specimens and for allowing the use of their host data. I also wish to thank: Robert Kula, Matthew Yoder, Beatrice Rodriguiz and Laurie Warriner (Texas A&M University) for stimulating discussions on parasitic Hymenoptera; the curators of the institutions mentioned in the Materials and methods section for assisting me with loans of specimens; Genevieve Jordan and my sons Riley and Stryker for patience and understanding while conducting this research. Michael Pogue and Thomas Henry (Systematic Entomology Laboratory, USDA/ARS), Mattias Forshage (Uppsala University, Sweden) and two additional anonymous reviewers improved the quality of this paper immensely. This project was funded by the National Science Foundation Partnerships for the Enhancement and Education in Taxonomy (PEET) Grant, number DEB9712543 and the Systematic Entomology Laboratory, USDA/ARS. Research was carried out at Texas A&M University, College Station, TX, U.S.A., Uppsala University, Uppsala, Sweden, and the United States National Museum, Smithsonian Institution, Washington DC.

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Accepted 20 September 2008

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