An integrated phylogenetic reassessment of the parasitoid superfamily Platygastroidea (Hymenoptera: Proctotrupomorpha) results in a revised familial classification

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Abstract. The superfamily Platygastroidea (Hymenoptera: Proctotrupomorpha) is a diverse group of parasitoid wasps that are parasitoids of nine orders of insects as well as spiders. They appear to show a clear pattern of host group specificity among genera. A robust phylogeny is essential for devising a stable and informative classification and understanding the pattern of the shifts to parasitize new host groups. We conducted phylogenetic analyses of Platygastroidea based on four molecular markers (18S, 28S, COI and wingless) and 119 morphological characters, and a phylogenomic analysis of a subset of taxa based on 4371 single-copy, protein-coding genes. The four-gene analyses, both with and without morphological data, robustly recovered some well-established groups, e.g., Platygastroidea in its traditional sense, Scelionini, Teleasinae and Telenominae, as well as some novel patterns of relationship. The ground-plan host for the superfamily are the eggs of Orthoptera, with multiple shifts to attack new host groups. The phylogenomic analysis of a subset of taxa recovered a clear pattern of relationships for the backbone of the superfamily with maximal bootstrap support. Based on the combination of these two approaches, we present a revised classification for Platygastroidea and recognize the following eight families: Geoscelionidae stat.rev., Janzenellidae fam.nov., Neuroscelionidae fam.nov., Nixoniidae stat.rev., Platygastroidea stat.rev., Proterosceliopsidae†, Scelionidae stat.rev. and Sparasionidae stat.rev.

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Introduction

Over the past decade, tremendous progress has been made in our understanding of the evolution and phylogeny of the insect order Hymenoptera (Sharkey, 2007; Heraty et al., 2011; Sharkey et al., 2012; Klopfstein et al., 2013; Peters et al., 2017). The order comprises more than 150,000 described species, and many are yet to be described (Aguiar et al., 2013). The evolution of sociality within the order has been the subject of close scrutiny (e.g., Branstetter et al., 2017), but this behavior is restricted to a single clade, the Aculenta. Most Hymenoptera are parasitoids, a life history in which the larval stages feed upon and eventually kill a single host arthropod. The most recent phylogenetic reconstruction of Hymenoptera proposed that diverse lineages of parasitoids – the Ceraphronoidea, Ichneumonoidea and Proctotrupomorpha – form a monophyletic group, dubbed the Parasitoida, and originated approximately 236 Ma (Peters et al., 2017).

The extant Proctotrupomorpha is composed of three lineages: Platygastroidea, Cynipoidea and a clade composed of the superfamilies Proctotrupoidea, Diaprioidea, Mymaromma-toidea and Chalcidoidea (Peters et al., 2017). The current study focuses on Platygastroidea, a diverse taxon with approximately 6000 species and 264 genera that are currently considered to be valid. A unique and distinctive feature of the superfamily are papillary sensilla (also known as multiporous sensilla) on the ventral surface of the apical antennomeres of the female (Bin, 1981). The presence of these sensilla enable the confident placement of most fossil amber inclusions of platygastroid females, with the oldest so far known pushing the age of the superfamily back at least to 120 Ma (Johnson et al., 2008).

Classifications of the 19th and early 20th centuries (e.g., Ashmead, 1893) placed the platygastroid wasps in a poorly defined group referred to as the Proctotrupoidea, Serphoioidae or Oxyura (with varying suffixes). The polyphyletic nature of the old ‘proctos’ is seen in the fact that today, while there remains a valid taxon called Proctotrupoidea, this is the depauperate remnant of a group whose members have since been dispatched to the superfamilies Ceraphronoidea, Chalcidoidea, Serphitoidea, Diapri-oidea, Chrysioidoea and Platygastridae. The Platygastroidea were first extracted from this taxonomic chaos by Masner (1956) under the name Scelionoidea. From 1930 until 2007 only two families of Platygastroidea were recognized, Scelionidae and Platygastriadae (often spelled Platygastridae). Species in the former were all egg parasitoids of either other insects – known hosts include species of the orders Odonata, Orthoptera, Mand-tegidae, Embiidiina, Hemiptera, Coleoptera, Neuroptera, Lepidoptera and Diptera – or spiders (citations in Table S1). The platygastriads also included a small number of species of egg parasitoids of beetles and auchenorrhynaceous Hemiptera (planthoppers), parasitoids of nymphal sternorrhynaceous Hemiptera (e.g., whiteflies, Aleyrodidae), as well as the anomalous Tetra-baeus Kieffer, gregarious endoparasitoids of larvae of Crabronidae (Hymenoptera). However, the great majority of species placed in the Platygastriadae were larval or egg-larval parasitoids of gall midges (Diptera: Cecidomyiidae). Thus, the two-family classification scheme roughly corresponded to significant biological differences.

Within the family Platygastriidae two main subfamilies were traditionally recognized, the Inostematinae and Platygastriinae, with a third subfamily sometimes added, the Sceliotrachelinae, until 1989 a monobasic subfamily endemic to South Africa. The Inostematinae and Platygastriinae were primarily distinguished by the presence or complete absence of fore wing venation, respectively. Masner & Huggert (1989) upended this increasingly precarious arrangement: they retained two subfamilies, Platygastriinae and Sceliotrachelinae, and distributed the genera of Inostematinae between them. Classification within the Scelionidae, with its greater species richness and morphological diversity, was more complicated. Three subfamilies were almost universally recognized, the Scelioninae, Teleasinae and Telenominae. Some authors, most recently Kononova & Kozlov (2001), also recognized the distinctive spider egg parasitoids as a separate subfamily, the Baeinae.

Valiant attempts were made to devise classifications at the tribal level within Platygastroidea, most notably those of Kozlov (1970) and Masner (1976). Many of the tribes, however, are monobasic: in the tribal scheme of Kozlov (1970), 20 of the 29 tribes of Platygastroidea contained only a single genus. Many of those that contained multiple genera, particularly the Callisce-lionini and Psilanteridini of the Scelioninae, are extraordinarily variable. The lack of practicality of the existing tribal classification is evidenced by the fact that a key to tribes has never been published.

The latter half of the 20th century was notable for the efficiency and effectiveness of new collecting techniques (Malaise traps, pan traps, flight-intercept traps, etc.), the tremendous increase in the number of specimens collected and deposited into museums and the geographic scope of collecting activities. The resulting dramatic increase in our understanding of the diversity of platygastroids made it clear that the existing classification was not capable of adequately absorbing the new taxa that were being discovered. The general adoption of the principles of phylogenetic classification also exposed the many weak points represented by paraphyletic and polyphyletic taxa. Few workers contested the validity of the monophyly of groups such as telenomines, telesinies, baeines and platygastriines. Other taxa, however, such as Scelioninae, Scelioninae and Inostematinae, were unsupportable. The problem within the scelionids was the lack of a viable alternative scheme of classification that remained true to the goal of monophyly, while also recognizing taxa that could be defined and recognized.

This was the situation upon the publication of the first explicit phylogenetic analysis covering the breadth of the superfamilly by Murphy et al. (2007). They analysed the nucleotide sequences of three markers, 18S and 28S ribosomal DNA (rDNA) and mitochondrial cytochrome oxidase I (COI), for ~70 in-group species representing 55 genera of Platygastroidea. These data strongly supported the hypothesis that the superfamily is a monophyletic group and that, within the superfamily, the classical Platygastroidea are also monophyletic. The latter group, however, arises from among genera that were traditionally grouped together as the Scelionidae, thus rendering the scelionids as a paraphyletic
taxon. Murphy et al. (2007) resisted the temptation to translate their work into a formal classification, recognizing the limitations in the scope of their conclusions inherent in the small number of DNA markers and restricted taxon sampling.

These limitations could not be imposed on other workers, however. With no additional analysis, Sharkey (2007) seized upon this paper as the basis for merging Scelionidae and Platygastridae into a single family, reasoning that Scelionidae was a paraphyletic taxon. This action glossed over two points: first, that Platygastridae in its traditional sense was supported as a monophyletic group, and, second, that except for only two genera – Neuroscelio Dodd and Archaeoteleia Masner, which together have a grand total of 24 species – all other scelionids in fact did group together in the Bayesian analysis of Murphy et al. (2007). Thus, complete elimination of the Scelionidae was not an unavoidable conclusion.

McKellar & Engel (2012) considered Sharkey’s single-family classification to be ‘retrograde’: ‘… a system in which much hierarchical as well as distinctive morphological and biological information is obscured’. Their solution was to resurrect the Platygastridae and Scelionidae as monophyletic families and segregate the Sparaspidae and Nixoidea into separate families. This reclassification appears to have relied on the intuitive tribal classification of Masner (1976) in which the monobasic tribe Nixoidea and Masner’s concept of the Sparasioni – the genera Archaeoteleia, Sparasion Latreille and Seliomorpha Ashmead – were raised to the level of family. Talmas et al. (2019) recently proposed a new family, Proterosceliopsidae, for the six species of the Cretaceous genus Proterosceliopsis Ortega-Blanco, McKellar & Engel. In summary, there are currently three competing family classifications for the extant species of Platygastroidea: (i) a single family, Platygastridae s.l.; (ii) two families, the Platygastridae and Scelionidae; and (iii) four families, the Platygastridae, Scelionidae, Nixoidea and Sparasionidae.

Returning to the analysis of Murphy et al. (2007), 90% of the genera traditionally placed in the Scelionidae clustered together in a maximally supported monophyletic group that they called the ‘main scelionid clade’. The analysis supported the hypothesis of monophyly for only a few named higher taxa within this clade: the tribe Scelionini and subfamilies Teleasinae and Telenominae. All other taxa above the rank of genus, at least those that were represented in the study by more than one genus, appeared as para- or polyphyletic groups. This corroborated an earlier molecular study that focused on the spider egg parasitoids in the tribe Baeini (Carey et al., 2006). Subsequently, Taekul et al. (2014) also found that one subgroup of the Telenomininae appeared to be more closely related to traditional members of the Scelioninae, concluding that even that morphologically well-defined subfamily was not monophyletic.

Murphy et al. (2007) represented a significant, but preliminary step forward in understanding platygastroid phylogeny. The goals of this study were to address the previous work’s weaknesses in both taxon and gene sampling, incorporate useful information from morphological data, and in doing so to develop a more robust resolution of relationships within the Platygastroidea. With a well-supported phylogeny, our goals were then to assess the pattern of host utilization among these wasps and to provide a new classification at the level of family that is both stable and informative.

Methods

All taxa, molecular and morphological data

Taxonomic sampling. A total of 166 species belonging to 93 genera of Platygastroidea were included in the analyses, together with four outgroups comprising one species each of Diprionidae, Megaspididae, Pteromalidae and Pelecinidae. The in-group included multiple representatives from all currently recognized platygastroid subfamilies and most tribes. Molecular voucher specimens were freshly collected from around the world. After nondestructive DNA extraction, each voucher specimen was assigned unique barcode and deposited in the C. A. Triplehorn Insect Collection (OSUC). Voucher information and GenBank accession numbers for markers included in the analyses are available in Table S1. Metadata for the voucher specimens included in this study can be accessed in the Hymenoptera Online database (https://mbd-db.asc.ohio-state.edu) using the identifiers (numbers prefixed with OSUC and USNMENT). Note that spaces in the identifiers are significant.

Molecular data. DNA was extracted from ethanol-preserved specimens (~70–95%) using the DNeasy Blood & Tissue Kit (Qiagen, Germantown, MD, U.S.A.; cat. Num. 69506), following the protocol used by Taekul et al. (2014). Four gene regions were amplified by PCR: two nuclear ribosomal (18S and 28S D2-3), one mitochondrial protein (COI) and one nuclear protein (wingless). These genes were selected for their variability and resolving power at different levels in Hymenoptera (Murphy et al., 2007; Heraty et al., 2011; Klopfstein et al., 2013).

Primers for PCR amplification are listed in Table 1. Two primers for amplification of an exon region of wingless, SceWgIF-1 and SceWgIR-1, were developed de novo for this study from existing Trissolcus basalis (Wollaston) genome sequences (Mao et al., 2012) using CLC Main Workbench. PCRs were carried out in 50 μL reactions containing 25 μL Taq® Green Master Mix 2X (Promega, USA), 0.5 μL of 100 μM primers, 21.5 μL H2O and 2.5 μL genomic DNA. Thermocycling conditions consisted of an initial denaturation at 94°C for 5 min, followed by 35 cycles of 1 min at 94°C, 1 min at the primer’s annealing temperature and 1.5 min of elongation at 72°C, ending with an additional extension of 72°C for 3 min. PCR products were purified using the QIAquick PCR purification kit (Qiagen) protocol when necessary. Amplicons were directly sequenced in both directions with forward and reverse primers by Beckman Coulter Genomics (Danvers, MA, U.S.A.). Chromatograms were assembled with SEQUENCER v4.0 (Gene Codes Corporation, Ann Arbor, MI, U.S.A.). The resulting sequences were deposited in GenBank (accession numbers begin with MF or MH) (Table S1).
Ribosomal sequences of 18S and 28S were aligned with MAFFT version 7.309 (Katoh & Standley, 2013) plugin in GENEIOUS 11.0.3, using the E-INS-i algorithm with all parameters at their default values. This algorithm has been shown to be the preferred alignment algorithm for ribosomal sequences of Hymenoptera (Munro et al., 2011; Klopfstein et al., 2013). Protein-coding genes (COI and wingless) were aligned by codon position using MUSCLE as implemented in MEGA7 (Tamura et al., 2013) and were realigned with MAF.TL as implemented in MEGA7 (Tamura et al., 2013) and were removed from the final analyses.

Morphological data. A dataset of 119 morphological characters was constructed for the in-group taxa (Appendix S1). These were derived from features traditionally thought to be valuable in recognizing relationships and classifying species, as well as those resulting from our efforts to find new morphological traits. Characters were scored based on the molecular voucher specimens or other specimens of the genus for which the specimens were badly damaged in the extraction process. Character data matrices were generated by a database application, vsyslab (http://vsyslab.osu.edu), designed to facilitate the production of taxon by character data matrices, and to integrate those data with the existing taxonomic and specimen-level database. All characters were treated as unordered. Inapplicable, unknown and multistate characters were coded with ‘?’. 

Phylogenetic analyses. We performed maximum likelihood (ML) analyses to infer relationships among platygastroids. ML analyses were performed in IQ-TREE (version 1.6.12; Nguyen et al., 2015). Two datasets were analysed: (i) the 4-gene molecular dataset (4G); and (ii) the 4-gene molecular + morphological dataset (4G + M). For these analyses, the concatenated alignment was partitioned by codon position for each protein-coding gene (COI and wingless) and each entire nuclear ribosomal gene (18S and 28S), resulting in eight initial partitions (Table 2; Chernomor et al., 2016). The best substitution model for each partition was estimated with MODELFINDER (Kalyaanamoorthy et al., 2017) using the MFP + MERGE command, which reduced the number of partitions to seven. Branch support was estimated with 1000 ultrafast bootstrap replicates (Hoang et al., 2018). We performed 25 independent tree searches for the 4G and 4G + M analyses and selected the single tree with the best (greatest) log-likelihood score. Neodiprion sertifer (Geoffroy) was used as the most distant outgroup in each analysis.

Genomic DNA was extracted from the whole body of single, ethanol-preserved specimens as described previously. Males were targeted for molecular data acquisition and processing. Genomic DNA was extracted from the whole body of single, ethanol-preserved specimens as described previously. Males were targeted for
extraction to limit the negative effects of heterozygosity on locus assembly (Yahav & Privman, 2019). For all specimens, excluding Ceratoteles Kozlov (added to the analysis later), library preparation and whole-genome sequencing were conducted at The Molecular and Cellular Imaging Center on the Wooster Campus of The Ohio State University. Libraries were prepared using a NEBNext® Ultra™ II DNA Library Prep Kit for Illumina® (New England Biolabs, Inc., Ipswich, MA, U.S.A.). Genomic DNA was sheared with a Covaris® S220 Focused-Ultrasonicator (Covaris, Inc., Woburn, MA, U.S.A.). Following shearing, size selection was performed with Pip- pin Prep (Sage Sciences, Inc., Beverly, MA, U.S.A.), and the 550–750bp fraction of each library was sequenced on the Illumina® MiSeq platform (Illumina, Inc., San Diego, CA, U.S.A.). Between three and six sample libraries were multi-plexed per MiSeq lane and paired-end sequences were generated with a MiSeq Reagent Kit v3 (600-cycles). DNA of Ceratotele- leas was sonicated to generate 350 bp fragments using S2/E210 Ultrasonicator (Covaris, Woburn, MA, U.S.A.). The fragments were subsequently end paired and nucleotide (A) overhangs were generated. Sequencing adapters were ligated using T4 DNA ligase. PCR was performed and products were then puri- fied and loaded onto an Illumina® NovaSeq 6000 (Illumina, Inc., San Diego, CA, U.S.A.) for paired-end sequencing according to the manufacturer’s recommendations.

The quality of the raw sequencing reads was determined using FASTQC (versions 0.11.5–0.11.8), ADAPTERREMOVAL (ver- sion 2.2.1; Schubert et al., 2016) was used to remove adapter sequences from the raw reads. The processed reads were then subjected to an additional round of FASTQC to ensure that exoge- nous sequences had been removed. The cleaned reads were then used in the assembly of orthologous loci. The raw sequencing reads were submitted to the NCBI SRA archive under BioProject accession number PRJNA550131: ‘Parasitoid wasps of the superfamily Platygastroidea (Hymenoptera, including Scelionidae and Platygastridae) – Genome sequencing and assembly’.

We identified single-copy, protein-coding genes in the genome of T. basalis by submitting its annotated set of protein-coding genes (Z. Lahey et al., unpublished data) to the orthodb v9.1 database (https://www.orthodb.org/v9.1/index.html; Zdobnov et al., 2017). Each T. basalis protein sequence was compared with those in the official gene sets (OGS) of four hymenopteran reference taxa, namely: Acromyrnex echinatior (Forel) (Formicidae), Athalia rosae (Linnaeus) (Tenthredinidae), Apis mellif- era Linnaeus (Apidae) and Orussus abietinus (Scopoli) (Orus- sidae). Of the 14 424 protein-coding genes identified in the T. basalis genome, orthodb v9.1 suggested 4736 to be present in single-copy based on a comparative analysis with the OGS of each reference taxon.

We used the automated Target Restricted Assembly Method (ATRAM; version 2.0.alpha.5; Allen et al., 2015, 2017) to assem- ble sequences orthologous to each of targeted single-copy, protein-coding genes in the 13 platygastroid and three outgroup taxa included in the phylogenomic analysis. ATRAM uses an iterative approach to assemble sequencing reads that match a target locus, such that the output of the first round is used as the input for the next, until (i) no new reads can be mapped to the contig or (ii) the user-defined number of iterations has been reached. We configured ATRAM to run for five iterations, and TRINITY (version 2.5.1; Grabherr et al., 2011) was used as the de novo assembler. Following the assembly of each locus, we utilized the atram-associated exon stitching pipeline (https://github.com/ juliena/exon_stitching) to splice together the exons of each locus for each taxon prior to phylogenetic inference. The steps involved in this pipeline are described by Allen et al. (2017).

We used the fastatranslate command of the program EXONRATE (version 2.4.0; Slater & Birney, 2005) to translate the output of ATRAM from nucleotides to amino acids. Premature stop codons within open reading frames were masked at the amino acid level with X. We then performed a reciprocal-best-BLAST following the methods of Allen et al. (2017). Briefly, we cre- ated a BLAST database of the 4736 single-copy, protein-coding genes from the T. basalis genome and used the translated ATRAM contig of each locus for each taxon as the query sequence. We performed this test to verify the orthology between the output of ATRAM and the protein sequences from T. basalis. Amino acid sequences from taxa that did not blast back to the correspond- ing protein in T. basalis as the top hit were not included in the phylogenetic analysis. Furthermore, we categorized the amino acid sequences of each taxon as either full-length or fragmented based on whether they were greater than or equal to half the length of the corresponding T. basalis ortholog or less than half its length, respectively. Only full-length amino acid sequences were used in the phylogenetic analysis.

Amino acid sequences of each gene were aligned with MAFFT (version 7.313–7.407; Katoh & Standley, 2013) using the l-ins-i algorithm. The resulting multiple sequence alignments were then concatenated and processed further to generate the final supermatrix using a custom bash script. The multiple sequence alignments included in the ‘full’ supermatrix were composed of genes (n = 4371) present in at least four of the 13 platygastroid taxa. A second ‘decisive’ supermatrix was also constructed composed of only those genes (n = 2607) that were present in at least one member of each focal group (i.e., outgroup, Neuroscelionidae, Nixoniidae, Platygastridae, Scelionidae and Sparasionidae).

**Phylogenetic analysis.** The phylogenetic analysis was con- ducted under ML using the program IQ-TREE (version 1.6.12; Nguyen et al., 2015). The supermatrix was partitioned by gene (Chernomor et al., 2016), and the best protein substitution model for each partition was estimated with MODELFINDER (Kalyaanamoorthy et al., 2017). MODELFINDER was run with the following command line options: -spp [partition file], -st AA, -m MF, -msub nuclear, -ms dayhoff, LG, WAG, DCMut, JTT, JTTDCMUT, -madd LG4X, LG4M. Details of these options are documented in the Command Reference section of the IQ-TREE documentation webpage (http://www.iqtree.org/ doc/). Branch support was estimated with 1000 ultrafast boot- strap replicates (Hoang et al., 2018), with the -bnni flag turned on to minimize the influence of potential model violations during phylogenetic tree building. We performed 10 independent tree searches and selected the tree with the best (greatest) log-likelihood score. Orussus was selected as the outgroup.

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Table 3. Sequence lengths and base frequencies for each gene used for phylogenetic reconstruction of the 4G dataset.

| Genes     | # Taxa | Sequence length (bp) | Base frequencies (%) |
|-----------|--------|----------------------|----------------------|
|           |        | Shortest | Longest | Average | A  | C  | G  | T  |
| 18S       | 152    | 533      | 957     | 673     | 24.8 | 21.9 | 28.1 | 25.1 |
| 28S       | 152    | 634      | 874     | 776     | 21.4 | 24.7 | 30.4 | 23.5 |
| COI       | 135    | 192      | 645     | 578     | 33.2 | 15.2 | 12   | 39.6 |
| wingless  | 99     | 240      | 489     | 464     | 23.2 | 26.4 | 29.5 | 20.9 |

based on its position within the order Hymenoptera (Peters et al., 2017).

Analysis of host association evolution

Host association was chosen for ancestral state reconstruction. We were interested in the pattern of changes of host associations among genera of wasps, specifically the associations at the level of host order (for the insect hosts, all spiders were treated as a single host group). We used the presumed ground-plan state of each genus for each terminal taxon. Each genus was scored based on the collecting information or information extracted from published literature and records stored in the Hymenoptera Online database (see Table S1). The genera Gryon Haliday and Telenomus have been reported to use several groups of hosts (e.g., Telenomus species are parasitoids of the eggs of Hemiptera, Lepidoptera, Diptera, and Neuroptera), but according to Taekul et al. (2014), the ground-plan hosts of both Gryon and Telenomus are likely to be Hemiptera. The ancestral states of host association were reconstructed on the 4G+M tree resulting from the analysis of concatenated data using both maximum parsimony and ML methods in Mesquite v3.61 (Maddison & Maddison, 2018). The phylogenetic tree from the 4G+M analysis was used to infer the ancestral host relationships for each taxon. Taxa without known host associations were excluded from the analysis.

Data deposition

The morphological and molecular matrices from the 4G, 4G+M and phylogenomic analyses, in addition to their corresponding partition and tree files, have been deposited in Dryad (Chen et al., 2021).

Results

Data properties

The 4-gene nucleotide data matrix consisted of 3662 aligned sites for 166 in-group taxa, of which 91 taxa had data for all loci; 17 lacked COI data; and 53 lacked wingless data. Sequence summary statistics are given in Table 3, including information on total/average length and base frequencies.

The full supermatrix for the phylogenomic analysis consisted of 2 444 345 amino acid sites split between 4371 partitions, one for each gene. The percentage of data missing from the supermatrix was 54%. The amount of missing data for each taxon was highly variable. Nixonia Masner had the lowest percentage of missing data (24.6%), whereas Amitus Haldeman had the highest percentage (81.9%). Sequences of nine taxa (seven platygastroids and two of the outgroups) had greater than 50% missing data or ambiguous sites (denoted in the alignment as an X). The atraM pipeline recovered approximately 3000 of the 4736 single-copy, protein-coding target sequences for each taxon after contig filtering. Trimorus Förster (Scelionidae: Teleasinae) was represented by the lowest number of sequences (1625), whereas Nixonia had the highest number (4184). The decisive supermatrix was composed of 2607 genes, 1 136 491 amino acid sites and 42% missing data.

Phylogenetic relationships

The results of the ML analysis of the combined morphological and four-gene data set are presented in Figs 1, 2. The results of the molecular-only analysis are shown in Figs 3, 4. We did analyse the morphological data independently in preliminary work. For reasons outlined in the discussion section, we are not presenting those results here.

Thirteen taxa and three outgroups were included in the phylogenomic study. We restricted representation of traditional platygastroids to the four genera Trichacis Förster, Amitus, Zelostemma Masner & Huggert, and Inostemma. Within the main scelionid clade, we included only four genera: Probarconus, Telenomus, Idris and Ceratoteleas. These correspond to the four scelionid subfamilies that can be found in the older literature: the Scelioninae, Telenominae, Baeinae and Teleasinae, respectively. Beyond these genera, we included one representative from Archaeoteleia, Sparasion and Sceliomorpha (corresponding to Sparasionidae sensu McKellar & Engel, 2012 and Sparasionini of Masner, 1976), Nixonia (Nixoniidae of McKellar & Engel, 2012 and Nixoniini of Masner, 1976) and the unplaced Neuroscelio. The first analysis was based on sequences from 4371 single-copy nuclear protein-coding genes. The results are presented in Fig. 5. All nodes received 100% ultrafast bootstrap support. We conducted a second analysis to assess the impact of including those genes that were missing for some taxa. This reduced, ‘decisive’ data matrix included only those genes that were present in at least one member of each family.
Fig. 1. Results of 4G+M maximum likelihood analysis of relationships within Platygastroidea, families other than Scelionidae. Colour codes refer to level of ultrafast bootstrap support values. Familial limits indicated on right.

and outgroup. This dataset comprised 2607 genes and a total of 1 136 491 sites. Of these, 41.2% of the individual sites had no data or were ambiguous. The resulting phylogeny followed the same protocol as the original dataset and produced identical results with all nodes maximally supported with the exception of the node subtending the outgroup pair of *Leptopilina* and *Trichopria* (Fig. S27, UFB 89/SH-aLRT 93.4).

**Host associations**

When host associations were mapped onto the ML tree from the concatenated 4G+M data set, both ML (Fig. 6) and maximum parsimony (Fig. S28) methods produced similar results. The most likely ancestral host for Platygastroidea is the eggs of Orthoptera. Ambiguous reconstructions are found at the node leading to the Platygastroidae and the node leading to the group of *Tiphodytes* + *Thoron*, both of which attack the eggs of aquatic Heteroptera and the Teleasinae, parasitoids of Carabidae.

**Discussion**

**Phylogenetic relationships**

Our results are based on data from two sources: morphology and DNA sequences. We analysed the morphological dataset alone, but we have not presented the results here. Whatever phylogenetic signal is inherent in the morphology appears to be swamped by noise, likely arising from several sources: character loss; parallel reductions, possibly because of the small size of these animals; parallel and convergent evolution in other characters; and, likely, errors in our hypotheses of homology.

Our rejection of the morphological analysis is based on two factors. First, the support values for many of the nodes in the analysis are extremely low. More troubling, however, is the failure of the morphological analysis to retrieve as monophyletic two clades that we think to be very well established and, more or less, can serve as internal controls: the traditional Platygastroidae and the Teleasinae. Setting aside their taxonomic rank, these are...
Fig. 2. Results of 4G + M maximum likelihood analysis of relationships within Platygastroidea, family Scelionidae. Colour codes refer to level of ultrafast bootstrap support values.
taxa that have been recognized for more than 150 years, are well
defined in terms of their structure and have proven to be robust
predictors of anatomical, molecular and biological characters.
The failure of the analysis of the anatomical data by themselves
to recover these two groups casts doubt on the reliability of the
other clades.

If the morphological data are unreliable, why include them at
all in a combined analysis with the sequence data? Our belief is
that in the appropriate context the phylogenetic signal in these
data can be detected and be influential. We defer to others the
question of whether, on theoretical grounds, such fundamentally
different types of data can or should be combined in a single
analysis.

Both the 4G + M (combined molecular and morphological
data, Figs 1, 2) and 4G (molecular data only, Figs 3, 4)
analyses corroborate many of the conclusions reported by
Murphy et al. (2007):

- The monophyly of the superfamily Platygastroidea.
- The monophyly of Platygastroidea in its traditional sense
  (from the year 1930 to 2007), comprising the subfamilies
  Platygastrinae and Sceliotrachelinae.
- The paraphyly of Scelionidae, in its traditional sense: the
  Platygastroidea arise within the traditional Scelionidae.
- The monophyly of the ‘main scelionid clade’ of Murphy
  et al. (2007), comprised of all traditional scelionids except the
  Spasarion, Nixoniini and the previously unplaced extant
genera Huddlestonium Polaszek & Johnson, Janzenella and
Neuroscelio.
- The paraphyly of the subfamily Scelioninae, as it subsumes
  both of the other two subfamilies, Telenominae and Teleas-
  ineae.
- The monophyly of Teleasinae.
- The monophyly of the Telenominae sensu Taekul
  et al. (2014).
- The tribes Baryconini, Calliscelionini and Psilanteridini are
  not monophyletic.

These hypotheses of monophyly all have high bootstrap
support in both analyses (>90%). To be clear, the bootstrap
values cited are ultrafast bootstraps that are reported to be
unbiased for values >70% (Minh et al., 2013).

Some novel relationships that emerge from both analyses
include the monophyly of a group made up of Nixonia and
Huddlestonium. Unfortunately, we were able to obtain very little
sequence data from Huddlestonium, an exceedingly rare group
that ranges from West to East Africa. Its likely closest relative,
Phylogeny and classification of Platygastroidea

Fig. 4. Results of 4G maximum likelihood analysis of relationships within Platygastridea, family Scelionidae. Colour codes refer to level of ultrafast bootstrap support values.

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the South American genus *Plaumannion*, is even less commonly encountered. Collecting fresh material of these genera would be one of the most important advances that would contribute to a better understanding of the phylogeny of the Platygastroidea.

Of comparable interest is the monophyletic group of *Neuroscelio + (Janzenella + Orwellium + traditional Platygastridae)*. In this case, although both analyses come to the same conclusion, the bootstrap support values are considerably lower. *Janzenella* is known from fossils, but live specimens have only been collected at a single locality in Costa Rica in the late 1980s. Therefore, the material available to us was not ideal in quality. We look forward to the results of a phylogenomic analysis based on ultraconserved elements that does include this pivotal genus (Talamas, personal communication). In this same grouping, both analyses confirm the close relationship of *Orwellium* with the traditional Platygastridae, consistent with the hypothesis put forward by Johnson et al. (2009).

The 4G and 4G + M analyses contradict each other on one important point: the relationship of *Archaeoteleia* to other platygastroids. Murphy et al. (2007) recovered a clade composed of *Archaeoteleia + Neuroscelio* that arises basal of the grouping of the traditional Platygastridae and the remaining traditional scelionids. Further, the platygastroids were placed as the sister group of (*Sparasion + Sceliomorpha*) + the remaining scelionids. In our molecular analysis, *Archaeoteleia* is recovered as the sister group to *Nixonia + Huddlestonium*. Adding the morphological data shifts its position to be the sister of *Sparasion + Sceliomorpha*, thus reifying the tribe Sparasionini (sensu Masner, 1976; Johnson et al., 2008) and Scelionidae of McKellar and Engel (2012).

This work modestly expanded the taxon sampling of traditional Platygastridae from 12 species in 11 genera to 17 species in 13 genera. The outcome was quite different from that of Murphy et al. (2007). They found that neither of the two subfamilies, Platygastridae and Sceliotrachelinae, were monophyletic. In the current analyses – except for the genus *Zelandonota* Masner & Huggert, which appears at the base of the platygastrid clade – Platygastridae and Sceliotrachelinae are both monophyletic. However, bootstrap support for this proposition is not robust, and more extensive taxon sampling is called for.

In Murphy et al. (2007), four species of the tribe Baeini (the spider egg parasitoids) in the genera *Baeus* Haliday, *Idris* Förster and *Ceratobaeus* Ashmead formed a monophyletic group. However, these species did not group together with the two other baeine genera, *Mirobaeoides* Dodd and *Neobaeus* Austin. Rather, the latter two were sister to the sole representative of the tribe Embidobiini, the genus *Embidoibia* Ashmead. This is the same result reported earlier by Carey et al. (2005). In the 4G + M analysis, Baeini in this restricted sense is also monophyletic (100% bootstrap support), but this group is sister to *Mirobaeoides + Neobaeus*, and this combination forms a monophyletic group that also includes the two embidobines, *Embidoibia* and *Echthrodesis* Masner (78% bootstrap support for the node combining all these taxa). This result suggests the reunification of the egg parasitoids of silk-using hosts, spiders (Baeini and *Echthrodesis*) and webspinners (the remaining Embidobiini), a tantalizing lead for investigating the mechanisms of host-finding in these wasps that is also corroborated by ongoing phylogenomic analyses (Z. Lahey, unpublished data).

Within the main scelionid clade are some additional groups with bootstrap support values ≥90%:

- **Probaryconus** Kieffer + *Oethecoctonus* Ashmead group together at the first bifurcation in the main scelionid clade in both the 4G and 4G + M analyses.
- **Duta** Nixon + *Holoteleia* Kieffer + *Spiniteleia* Masner + *Masnerella* Özdikmen form a monophyletic group in the 4G + M analysis. They also group together in the 4G results, but with lower support. These genera are typically, but not exclusively, associated with grassy, open habitats.
Fig. 6. Maximum likelihood ancestral state reconstruction of host relationships of Platygastroidea. All hosts are in the egg stage, except that *Amitus* are parasitoids of nymphal whiteflies, and platygastrines are both egg-larval and larval parasitoids of gall midges.
• **Macroteleia** Kieffer + **Triteleia** Kieffer: two very common genera, especially in the tropics, that are parasitoids of Tettigonoidae.

• Genera placed near to or synonymized with **Opisthacantha** Ashmead by Masner (1976) that possess a **Ceratobaeus**-type ovipositor (i.e., an appendicular ovipositor with direct musculature). These are represented here by the names **Opisthacantha**, **Elgonia** Risbec and **Lapitha** Ashmead.

• **Apegus Förster** + **Baryconus** Förster: part of the tribe Baryconini.

Our results offer scant guidance for how one might organize the diversity within the main scelionid clade into a tribal classification. The best supported groupings, corresponding largely to Telenomini, Teleasmini, Baeini and Scelionini, were already well established. The problematic Baryconini, Pisanteridini and Calliscelionini do not form coherent groupings, nor is an alternative arrangement apparent.

Morphological characters that have traditionally thought to be important in platygastroid classification and relationships include the so-called submarginal ridge of the metasoma, the number of antennomeres, the presence of a skaphion, the tibial spur formula and the structure of the ovipositor. Our analyses illustrate well the mixed messages coming from these features.

The submarginal ridge is formed from the differentiation of narrow laterotergites and laterosternites on the metasoma and their flexion and articulation. This is most clearly seen from below (Fig. 9C). Of the taxa in Figs 1–4, this feature is characteristic of the Sparasionini sensu Masner, **Nixonia**, **Neuroscelio** and most of the main scelionid clade. It is absent from the platygastroids, **Janzenella** and **Huddlestonium**. However, it is also convergently absent in the telenomines (∼900 species), male **Baeus** and some species of **Tiphodytes** and **Aradophagus**.

The tibial spur formula, more specifically, the number of mid and hind tibial spurs, is more conservative. The plesiomorphic condition is likely two tibial spurs on both the mid and hind legs. This number is reduced to one in **Huddlestonium**, numerous species of platygastroids and all species of the main scelionid clade. In **Janzenella**, there is one spur on the mid tibia and two on the hind.

The skaphion appears as a medial sclerite at the anterior margin of the mesoscutum. In its most well-developed form, the posterior margin is distinct, and its sculpture differs from that of the rest of the mesoscutum (typically it is smooth and shining). Internally, the skaphion is found within the anterior area of attachment of the dorsal longitudinal muscles, and it seems reasonable to speculate that it is somehow involved with the wasps’ indirect flight mechanism. The potential value of the skaphion in inferring relationships was first proposed by Kozlov (1970) and subsequently elaborated by Masner (1972, 1976). At times, this can be a difficult feature to recognize because the anterior portion of the mesoscutum is commonly flexed downward to articulate with the pronotum, the posterior margin may be poorly delimited and the sculptural differences slight. In our view, the skaphion is found only within the main scelionid clade. Engel et al. (2017) asserted that it is present in the Cretaceous **Geoscelio** Engel & Huang, but our interpretation of the image leads us to the opposite conclusion. Within the main scelionid clade, however, some groups never have a skaphion: the telenomines, teleasines, Scelionini and the complex of **Probaryconus** + **Oethecocnous**. Beyond that, however, this character appears or disappears without any apparent rhyme or reason. In fact, it is not consistently present in the range of species in some genera (such as **Lapitha** and **Caloteleia**). Perhaps within a particular narrow context the skaphion may be a phylogenetically informative character, but its value as such for the main scelionid clade is hard to discern.

One of the most spectacular characters of many genera is the elongate, telescoping ovipositor, dubbed the **Scelio**-type ovipositor by Austin & Field (1997). In some cases, the membranous tube that can be everted from the posterior end of the body can be 2–3 times the length of the metasoma. Austin & Field (1997) concluded that the **Scelio**-type ovipositor was an apomorphic condition, with the so-called **Ceratobaeus**-type ovipositor being the ground-plan state for the Platygastroidea as a whole. They further suggested that the joint possession of the **Scelio**-type ovipositor may define a monophyletic group that they provisionally called the Scelionini sensu lato. Talamas et al. (2017) described two superficially similar tubular ovipositor systems in **Gastrotyposes** Brues and **Platygaster** Latreille of the traditional Platygastroidea but provided convincing evidence that these are convergences. They treated the presence of a **Scelio**-type ovipositor in **Archaeoteleia** and the main scelionid clade as the independent evolution of remarkably similar character systems, an interpretation that is consistent with the results we present here. However, they also posited a single derivation of this character system within the main scelionid clade. In our results, this character appears to be part of the ground-plan of the main scelionid clade, but within that group there is such a bewildering pattern of its presence (and recurrence of the **Ceratobaeus**-type ovipositor) that it leads us to suspect that the so-called **Scelio**-type ovipositor is much more complex than we can yet appreciate. This suspicion echoes the cautious approaches of those who have studied the structure closely (Austin & Field, 1997; Talamas et al., 2017).

Finally, one of the classical morphological characters used in the Platygastroidea is the number of antennomeres. The possession of 14 antennomeres is typically thought to be the plesiomorphic condition, as it is found in the extant genus **Nixonia** as well as the fossil genera **Archaeoscelio**, **Proteroscelio**, **Proterosceliopsis** and **Geoscelio**. That number was subsequently reduced to 12 in **Sparasion**, **Sceliomorpha**, **Archaeoteleia**, **Neuroscelio** and as the ground-plan state in the main scelionid clade. **Huddlestonium**, known only from females, has 13 antennomeres. Beyond this, however, there seems to have been further, nearly rampant reductions in the number of segments in **Janzenella**, all platygastroids and within the main scelionid clade in the telenomines, Scelionini (sensu stricto), baeines, embidobiines and occasionally in other genera. Beyond the taxa included in our analysis, other notable examples of antennomere reduction are found in the genera **Plumannion** and **Cobaloscelio** Johnson & Masner. In some cases, the reduction in antennomere number is asymmetrical between the sexes. Male telenomines (with one or two exceptions) have 12 antennomeres, whereas the females...
have 10 or, most commonly, 11. Conversely, female Scelionini have 12, and the males 10. These are two examples where the morphological features appear to provide strong evidence for relationships, supporting our decision to include them in the 4G+M analysis.

Overall, we are encouraged by these results (the ‘glass half-full’ perspective). We can more clearly see the pattern of relationships within the superfamily and use these results to interpret the evolution of host relationships (discussed below) and some of the morphological peculiarities of these wasps. On the other hand, we were only able to generate data from a single nuclear protein-coding gene (wingless) from enough taxa to include those data in the analyses. It is apparent that there is still a good deal of uncertainty of relationships, particularly within the main scelionid clade. Additionally, several critical nodes near the base of the phylogeny do not have high enough bootstrap support values to give us great confidence in their stability. This led us to adopt the second, phylogenomic approach to the question.

**Phylogenomic analysis**

We were particularly keen to develop a robust hypothesis of relationships in the ‘backbone’ of the cladogram to help devise a workable familial classification of Platygastroidea. By ‘backbone’ we mean the relationships between the main scelionid clade, the platygastroids, the sparsasionines and the unplaced genera Neuroscelio, Nixonia, Janzenella and Huddlestonium. The initial 4G and 4G+M analyses did not provide the desired confidence level and resolution in the pattern of relationships (Figs 1–4). Therefore, we adopted a phylogenomic approach so as to more robustly resolve these relationships. We increased the number of genetic markers used by more than two orders of magnitude, thus seeking to increase the phylogenetic signal-to-noise ratio. The tradeoff for this expansion in markers, however, was that some interesting and potentially important taxa were recovered as sister taxa, with the Platygastriidae sister to them. A clade corresponding to Sparasionini was recovered as sister taxon to the main scelionid clade. The tree topology derived from the phylogenomic analysis mirrors that of the 4G+M analysis with two major differences, the positions of Sparasionini and Nixonia. We have much greater confidence in the placement of these taxa based on the phylogenomic analysis due to the sheer scale of the dataset and the fact that, in subsequent work, their phylogenetic position has remained stable under increased taxon sampling (Z. Lahey, unpublished data).

**Host associations**

Platygastroids use nine orders of insects as well as spiders as hosts (Table S1). There are many host records, both in the published literature and on labels attached to specimens, that purport to have reared platygastroids from some very unlikely hosts. Our characterization of host relationships here reflects the bulk of known records. Several taxa (possibly clades) were earlier noted to be associated with specific hosts (Austin & Field, 1997; Austin et al., 2005; Taekul et al., 2014). This pattern of host group specificity led Austin et al. (2005) to raise several interesting questions regarding the evolution of host associations. However, the absence of any phylogenetic scheme for higher-level taxa made it impossible to suggest answers beyond informed speculation. Host associations have been recorded for 51 of the 96 in-group genera (53%) in this study. With a phylogeny in hand, we can begin to interpret the evolution of host relationships within the superfamily.

Austin et al. (2005) suggested that Orthoptera is likely to be the plesiomorphic host group for the superfamily given that it is the order most commonly used across the Scelioninae and is the host group of the genera Archaeoteleia, Nixonia and Sparasion. Our current results support this hypothesis. Archaeoteleia, Nixonia and Sparasion all are egg parasitoids of Orthoptera. In addition, a basal genus of the main scelionid clade, Oethocotomus, also parasitizes orthopteran eggs. Although the relationships within the main scelionid clade are not all well supported, orthopteran egg parasitism is commonly found in several genera (Fig. 6; Table S1).

Individual groups of platygastroids have undergone subsequent changes to attack different arthropod groups. Platygastriinae and Sceliotrachelinae have shifted to parasitize Diptera, Hemiptera, Hymenoptera and Coleoptera. Platygastriinae likely only parasitize Diptera, Hemiptera, Hymenoptera and Coleoptera. Platygastrinae and Sceliotrachelinae have shifted to parasitize Diptera, Hemiptera, Hymenoptera and Coleoptera. Platygastrinae and Sceliotrachelinae have shifted to parasitize Diptera, Hemiptera, Hymenoptera and Coleoptera. Platygastrinae likely only parasitize gall midges (Diptera). Aradophagus Ashmead, all members of the Baeini s. str. (with one known exception, Lomeli-Flores et al., 2019) and Echthrodesis (Embobiini) are parasitoids of spider eggs. As discussed above, Baeini and Embobiini may be closely related. If this is the case, because eggs of both spiders and Embidina are usually covered by or associated with silk, it suggests that these wasps may share a common evolutionary history of silk searching (Galloway & Austin, 1984), and therefore use similar mechanisms to locate host eggs. Yoder et al. (2009) suggested that the host of Axea Masner & Johnson is Mantodea because a long series of specimens is labelled as ‘ex oothéque Phasmatidae’, but walking sticks were not thought to produce oothecae. A recent study, however, found that some Phasmatoidea do produce oothecae (Goldberg et al., 2015). Therefore, the hosts for Axea could be either Mantodea or Phasmatoidea. In either case, a close relationship between Axea and Mantibaria (species of which are parasitoids of mantis eggs) is not supported by our results. Thoron and Tiphodytes (Thoronini and Tiphodytini) are parasitoids of aquatic Hemiptera (Nepidae and Gerridae, respectively). Teleasinae are known only to parasitize the eggs of Coleoptera (Carabidae). Host shifts within Telenominae were more extensively discussed by Taekul et al.
et al. (2014). Briefly, the plesiomorphic hosts of these wasps appear to be terrestrial Hymenoptera, from which shifts have been made to attack Lepidoptera, Diptera and Neuroptera (Taekul et al., 2014).

In summary, major groups within the superfamily have shifted from attacking Orthoptera to Diptera on two occasions; at least twice to Coleoptera; spiders two to three times; Embiidina once; Odonata one to two times; Mantodea one to two times; perhaps to Phasmatodea; aquatic Hymenoptera once; terrestrial Hymenoptera at least three times; Lepidoptera twice; and to Neuroptera once (Taekul et al., 2014). Two observations are noteworthy: no single species is yet known to attack hosts in more than one order, and at least half of these shifts are correlated with massive radiations of species. For example, Platygastrinae comprise more than 1800 species and are restricted to the eggs or larvae of gall midges. Similarly, the shifts of Teleasinae to Coleoptera, Bacinii to spiders, and of Grynini + Telenominae to terrestrial bugs and then to Lepidoptera, Diptera and Neuroptera are correlated with radiations of each group into several hundreds or thousands of species.

The correlations between host shifts and radiations suggest the possibility of a causal relationship. Abundant evidence has indicated that platygastroids rely on semiochemicals (e.g., sex and aggregation pheromones, cuticular hydrocarbons, female reproductive accessory gland secretions as well as plant-produced chemosensory capacity may be a critical factor in shifting to a new group of hosts, and this may open the door to an explosion of new species exploiting this new resource. To critically explore this suggestion, a robust hypothesis of phylogenetic relationships is necessary. The results we present here are a step in that direction. The taxon sampling is fairly extensive in this study, and more taxon sampling for the 4G + M analysis seems unlikely to contribute to the resolution of relationships, at least those within the main scelionid clade. Increasing the representation of taxa in the phylogenomic analysis probably holds the best prospects for future progress.

Revised familial classification of Platygastroidea

Geoscelionidae Engel & Huang, 2017 stat.rev. (Figs 7A, B, 9A, B).

Geoscelionini Engel & Huang, 2017: 7 (original description; diagnosis; figured).

Type genus. Geoscelio1 Engel & Huang.

Included genera. Archaeoscelio1 Brues, Cobaloscelio1 Johnson & Masner, Geoscelio1 Engel & Huang, Huddlestonion Polaszek & Johnson, Plaumannion Masner & Johnson.

Female antenna with 10–12 flagellomeres; male antenna with sex segment on A5 and possibly A4 (males known only for Cobaloscelio1); frontal depression absent; malar sulcus absent, except in Geoscelio1; pronotal cervical sulcus without setation; mesoscutum distinctly wider than long in dorsal view; transverse lamina on mesepisternum absent; mesepimeral sulcus present; in winged forms R continuous with more distal venation, r-rs of fore wing (stigmal vein) very short, diverging from R1 submarginally, R1 does not extend as far as the costal margin (images in Masner et al., 2007); tibial spur formula 1–2–2 or 1–1–1; metasoma without apparent laterotergites; T1–T3 strongly transverse, subequal in length; anterior margin of T1–T5 and S1–S5 with row of strong foveae; where visible, S1 with median longitudinal keel, and S1 is produced anteriorly to extend between the hind coxa (unclear in Geoscelio1).

Remarks. Engel et al. (2017) originally described this taxon as a tribe for the monobasic Cretaceous genus Geoscelio1. They recognized similarities with Archaeoscelio1 but placed considerable emphasis on the tibial spur formula (1–2–2 in Geoscelio1, 1–1–1 in Archaeoscelio1) as justification for excluding Archaeoscelio from Geoscelionini. Although this character is invariant (1–1–1) in the many genera making up the Scelionidae (that is, within the main scelionid clade), it varies among and even within genera of traditional Platygastroidea. Therefore, this single character should not be considered dispositive. The biology is unknown for the included genera. The three extant species have been collected in south-eastern Brazil (Plaumannion fritzi Masner & Johnson, Venezuela (Plaumannion yepezi García) and Africa, from Côte d’Ivoire east to Kenya (Huddlestonion exa Polaszek & Johnson).

Janzenellidae Johnson & Austin, fam.nov. (Figs 7F, G, 14A).

http://zoobank.org/urn:lsid:zoobank.org:act:67B305C4-A05C-472B-9B89-E40D82E3BE2D

Type genus. Janzenella Masner & Johnson.

Included genera. Janzenella Masner & Johnson.

Female antenna with nine flagellomeres; frontal depression absent; malar sulcus absent; pronotal cervical sulcus without setation; mesoscutum approximately as wide as long; transverse lamina on mesepisternum absent; mesepimeral sulcus present; R in fore wing continuous with more distal venation, r-s of fore wing (stigmal vein) very short, arising from small, nearly punctiform C+R (marginal vein, images in Masner & Johnson, 2007); tibial spur formula 1–1–2; metasoma with broad laterotergites; T1–T3 subequal in length; sutures

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Fig. 7. Habitus images of exemplar taxa of the families Geoscelionidae, Nixoniidae, Neuroscelionidae and Janzenellidet. Geoscelionidae (A) Huddlestonium exu Polaszek & Johnson (OSUC 232305), posterodorsal view; (B) Plaumannion fritzi Masner & Johnson (OSUC 146569), dorsal view. Nixoniidae (C) Nixoniakrombeini Johnson & Masner (OSUC 146429), dorsal view. Neuroscelionidae (D) Neurosceliododdi Galloway, Austin, & Masner (OSUC 147252), dorsal view; (E) lateral view. Janzenellidet (F) Janzenellainnupta Masner & Johnson (OSUC 264384), dorsal view; (G) lateral view. Scale bars in millimetres.
between metasomal tergites and sternites simple, without distinct, large foveae along anterior margins; S1 not produced anteriorly between hind coxae.

Remarks. *Jansenella innupta*, the only known species, is a minute, strongly depressed species. At a glance, it resembles a bethylid or an elongate telenomine, but closer examination will reveal the significant differences. This species is known only from the female sex. Fresh material has been collected only from a single locality in Costa Rica. The same species is also recorded from Dominican amber (Oligocene – Miocene, Masner & Johnson, 2007). The biology of *J. innupta* is unknown.

**Neuroscelionidae Johnson & Austin, fam.nov.** (Figs 7D, E, 13B).

http://zoobank.org/urn:lsid:zoobank.org:act:7252CAC5-C0C3-4014-9866-BD5DFA6C6252

Type genus. Neuroscelio Dodd.

Included genera. Brachyscelio1 Brues, Cenomanoscelio1 Schlüter, Neuroscelio Dodd.

Female antenna with 10 flagellomeres; male antenna without apparent sex segment or tyloids; frontal depression absent; malar sulcus absent; pronotal cervical sulcus without setation; mesoscutum approximately as wide as long; transepisternal line on mesepisternum absent; mesepimeral sulcus present; R in fore wing continuous with more distal venation, r-rs (stigma vein) in fore wing elongate, arising from a distinct marginal vein (C + R); tibial spur formula 1–2–2; metasoma with distinct, narrow laterotergites; T1 and T2 subequal in length, or T2 slightly longer than T1, T3 distinctly shorter than T2 and strongly transverse; sutures between metasomal tergites and sternites simple, without distinct, large foveae along anterior margins; S1 with median longitudinal keel, but not produced anteriorly.

Remarks. Species in this family are not particularly striking, appearing similar in size and habitus to many gryonines and telenomines. They have a well-developed stigmal vein, a feature otherwise found only in Scelionidae, Sparasionidae and the genus *Orwellium*. The two fossil genera, *Brachyscelio* (Eocene) and *Cenomanoscelio* (Cretaceous) are placed here based on their descriptions in the literature (Brues 1940; Schlüter 1978). The type material is either lost or otherwise unavailable. *Neuroscelio* is typically collected in forests and is known from Australia, Vietnam, Thailand and Malaysia (Sarawak). The biology of this interesting group is still undiscovered.

**Nixoniidae Masner. 1976 stat.rev.** (Figs 7C, 11A, B, 12F).

Nixonini Masner, 1976: 11 (original description; diagnosis).

Type genus. *Nixonia* Masner.

Included genera. *Nixonia* Masner.

Female antenna with 12 flagellomeres; male antenna with tyloids on A4–A5, sometimes with additional tyloids on subsequent antennomeres up to a maximum of A8; frontal depression absent; malar sulcus absent; pronotal cervical sulcus setose; mesoscutum approximately as wide as long; transepisternal line on mesepisternum absent; mesepimeral sulcus present; R continuous with more distal venation, r-rs in fore wing moderately long, diverging from R submarginally, R1 short, not reaching costal margin (i.e., no marginal vein); tibial spur formula 1–2–2; metasoma with distinct, narrow laterotergites; T1–T3 subequal in length; sutures between metasomal tergites and sternites with transverse depressions; S1 not laterally compressed, not extending forward between hind coxae.

Remarks. *Nixonia* is one of the largest platygastroids, with the body up to 9 mm long. They may be immediately recognized among extant platygastroids by their 14-merous antennae (in both sexes). The females also have the apical tergite (T6) dorsoventrally flattened with a notched apical margin. Females are also notable for being the only platygastroids in which the paired papillary sensilla on the antenna are arranged in transverse pairs on each antennomere, rather than the typical end-to-end arrangement in all other known species. *Nixonia* is widespread in sub-Saharan Africa, Egypt, Somalia, India, Sri Lanka and southeast Asia. The host of one species, *N. watshami* Johnson & Masner, is known: the eggs of the armoured bush cricket, *Acanthoplus discosoidalis* (Walker) (Orthoptera: Tettigoniidae, Hetrodinae).

**Platygastridae Haliday, 1833 stat.rev.** (Figs 8A, B, 9D, 10A, 12C).

Platygastridae Haliday, 1833: 269 (original description).

Type genus. Platygaster Latreille.

Included genera. Sixty-nine genera (extant and fossil), including *Orwellium* Johnson, Masner & Musetti. See Masner (1979), Masner & Huggert (1979) and Vlug (1995) for full listing of the included genera.

Female antenna with 5–8 flagellomeres; male antenna with single sex segment on A4 or A5; frontal depression absent; malar sulcus present or absent; pronotal cervical sulcus with or without setation; mesoscutum approximately as wide as long; transepisternal line on mesepisternum present or absent; mesepimeral sulcus absent; in winged forms, r-rs usually absent, if present usually extremely short, R1 when present very short, not reaching costal margin, in *Orwellium* apex of R in fore wing continuous with more distal venation, r-rs moderately elongate, arising from short C + R (marginal vein); tibial spur formula 1–1–1, 1–1–2, 1–2–2; metasoma with distinct laterotergites, either broad or narrow; T2 distinctly the longest metasomal tergite; sutures between metasomal tergites and sternites simple, lacking foveae along anterior margin, or with foveae only at anterior margins of T1 and T2; S1 not laterally compressed, typically not protruding anteriorly between hind coxae (sometimes the so-called foamy structures may protrude between the hind coxae).

Remarks. Platygastridae is a remarkably species-rich taxon, generally characterized by their minute size (typically ~1 mm in length) and reduction in the number of antennomeres, wing venation, number of metasomal segments and overall body sculpture. Although the body of most species is almost mirror-like smooth or with only very shallowly incised microsculpture, there are some noteworthy exceptions. The inclusion of *Orwellium* in the family stretches its definition, and further sequencing of this genus is needed to be more confident of the details of its position in the tree. As far as is known, most species are larval or egg-larval parasitoids of Cecidomyiidae (gall midges). The subfamily Sceliotrachelinae is more biologically diverse and has been reared from the eggs.
Fig. 8. Habitus images of exemplar taxa of the families Platygastroidea, Proterosceliopsidae, Sparasionidae and Scelionidae. Platygastroidea (A) Platygaster kimballi MacGown (USNMENT01059221), lateral view (Platygastrinae); (B) Sceliotrachelus braunsi Brues (SAM-HYM-P030894), dorsal view (Sceliotrachelininae). Proterosceliopsidae (C) Proterosceliopsis plurima Talamas, lateral view. Sparasionidae (D) Archaeoteleia gilbertae early (OSUC 179074), dorsal view; (E) Sparasion sp. (OSUC 261919), lateral view. Scelionidae (F) Baeus sp. (OSUC 243317), lateral view; (G) Thoron metallicus Haliday (USNMENT01109400), lateral view; (H) Acantholapitha sp. (OSUC 243317), dorsal view; (I) Lapitha sp. (USNMENT01197887), dorsal view; (J) Ceratobaeus sp. (USNMENT01335140), lateral view; (K) Triteleia sp. (USOC 225498), dorsal view (images F–K Scelioninae); (L) Telenomus goliathus Johnson (USNMENT00903175), lateral view (Telenominae); (M) Trimorus sp. (USNMENT01223632), lateral view (Telesinae). Scale bars in millimetres.
of Coleoptera and auchenorrhynous Hemiptera, the nymphs of sternorrhynous Hemiptera, and (remarkably) the larvae of crabronid wasps. The family is found worldwide and is very abundant both in species and individuals.

**Proterosceliopsideae** Talamas, Johnson, Shih & Ren, 2019 (Figs 8C, 12A).

Proterosceliopsideae Talamas, Johnson, Shih & Ren, 2019: 20 (original description).

Type genus. *Proteroscelio* Ortega-Blanco, McKellar & Engel.

Included genera. *Proteroscelio* Ortega-Blanco, McKellar & Engel.

Female antenna with 12–13 flagellomeres; frontal depression absent; malar sulcus present; pronotal cervical sulcus setose; mesoscutum approximately as long as wide; transepisternal line on mesepisternum present; mesepimeral sulcus present; apex of R in fore wing gap (bulla) separating it from more distal venation, r-rs in fore wing elongate, arising from marginal vein; tibial spur formula 1–2-2; metasoma with distinct narrow laterotergites; T1–T3 subequal in size; sutures between metasomal segments 1–5 with transverse depressions; S1 not mediately keeled, not projecting anteriorly between the hind coxae.

Remarks. This family is known from Cretaceous amber inclusions (Myanmar, Álava). The presence of the transepisternal line suggests a relationship with the Platygastridae, the only other family in which the character is found.

**Sclionidae Haliday, 1839** stat.rev. (Figs 8F–M, 9C, 10B, 11D, 12D, E, 14B).

Sclionidae Haliday 1839: ii (original description; keyed).

Type genus. *Scelio* Latreille.

Included genera. Currently 176 genera (extant and fossil). See Johnson (1992) for listing of genera then currently valid and http://hol.osu.edu for current status.

Female antenna with 5–10 flagellomeres; male antenna with sex segment on A5, occasionally no differentiated structure apparent; frontal depression usually present; malar sulcus present; pronotal cervical sulcus without setation; mesoscutum usually about as long as wide; transepisternal line on mesepisternum absent; mesepimeral sulcus present (with the single exception of *Aneuroscelio* Kieffer); in winged forms apex of R continuous with more distal venation, r-rs elongate, arising from marginal vein of varying length, some species with venation entirely lost or with only very short spur of R at base of wing; tibial spur formula 1–1–1; metasoma with distinct laterotergites, either broad or narrow; relative size of metasomal segments variable; sutures between metasomal tergites and between sternites variable, usually either simple or with a row of foveae along anterior margin limited to the first two or three segments; S1 usually not mediately keeled, not projecting anteriorly between the hind coxae.

Remarks. In this revised sense, the Sclionidae largely corresponds to the family as it was conceived prior to 2007. The differences are in the exclusion of 15 genera, only one of which (*Sparasion*) has any significant presence in the literature. In all analyses the main scelionid clade, first recognized by Murphy et al. (2007), is recovered with maximal support.

All the subfamilies that have traditionally been recognized, save one, the Scelioninae, are also recovered. However, there is no clear pathway to a clean subdivision of the family into monophyletic subfamilies based on the present data and analyses.

The Scelionidae has the greatest diversity of hosts in the superfamily and most biological data in general. The Telenominae, particularly the genera *Trissolcus* Ashmead and *Telenomus* Haliday, have been extensively studied because of their role as biological control agents of their hosts. Sclionids are found worldwide, from the shores of the Arctic Ocean to the southernmost reaches of South America and New Zealand. In this revised sense, the family is known only as far back as the Eocene, and at that time the group was already abundant and diverse.

**Sparasionidae**, Dahlbom, 1858 stat.rev. (Fig. 8D, E, 11C, 13A).

Sparasionidae Dahlbom, 1858: 290 (original description; diagnosis).

Type genus. *Sparasion* Latreille.

Included genera. *Archaeoteleia* Masner, *Electroteleia* Brues, *Mexon* Masner & Johnson, *Listron* Musetti & Johnson, *Scelionomorpha* Ashmead, *Sparasion* Latreille.

Female antenna with 10 flagellomeres; male antenna with tyloids on A4, usually with additional tyloids on subsequent segments up to A11; frontal depression absent; malar sulcus usually absent; pronotal cervical sulcus without setation; mesoscutum about as wide as long; transepisternal line on mesepisternum absent; mesepimeral sulcus present; in fully winged forms apex of R in fore wing separated from more distal venation by a distinct bulla (gap), r-rs in fore wing elongate, recurved, arising submarginally; R1 extending to costal margin of fore wing, often enlarged to form what appears as a stigma; tibial spur formula 1–2–2; metasoma with distinct, narrow laterotergites; T1–T3 subequal in length; punctures at anterior margins of metasomal segments 2–5 present; S1 mediately keeled, anterior margin extended forward between hind coxae.

Remarks. Sparasionids include some of the largest species of platygastroids (up to 12 mm in length), comparable in length to *Nixonia* and the most elongate species of *Triteleia* Kieffer (*Sclionidae*). The genus *Sparasion* is particularly rich in species in the Palearctic region. Aside from a small number of brachypterous forms, sparasionids can be immediately diagnosed by the presence of a bulla in the fore wing, a gap between the apex of the submarginal vein (R) and more distal venation. Several species are noteworthy for their metallic colour, most strongly expressed in species of *Sparasion* from southeast Asia. Many species of *Scelionomorpha* have their mesosoma and metasoma with extensive red or yellow colours. Little is known about the hosts of Sparasionidae. *Sparasion* in the Nearctic have been reared from the eggs of Tettigonioidea, and *Archaeoteleia* from New Zealand parasitize the eggs of wetas (giant flightless crickets: *Rhaphidophoridae*). The geographic distribution of the extant genera is intriguing. *Archaeoteleia* has a trans-Antarctic distribution, occurring in Chile and New Zealand. Species of *Sparasion* occur in the Nearctic, Palearctic, Afrotropical and Oriental regions, but they are entirely absent from the Neotropics and Australasia.
The remaining extant genera are found only in the New World, from the southernmost United States to Chile (but not in the West Indies). Sparasionids are present in the fossil record from the Cretaceous period (Burmese amber, Talamas et al., 2017).

**Comments on the new family classification**

Our evaluation of the best way to translate our phylogenetic hypothesis into a classification was guided by three principles. First, all taxa that are to be formally recognized should be monophyletic; second, family-level taxa should be diagnosable based on morphological characters; and third, given a choice, we prefer not to recognize monobasic taxa. The reasoning behind the first principle is obvious. We include the second guideline because in practical everyday use in entomology, the rank of family is the ‘coin of the realm’, the basic unit with which insect scientists of all subdisciplines communicate. This practical perspective is reflected in the common requirement of entomological journals that the names of species and genera be accompanied by the specification of the order and family in which they are placed. The third guideline, perhaps more of a preference, is based on the fact that a monobasic taxon does not add to the capacity of a classification to provide a predictive framework or to serve as an information storage/retrieval system, being redundant with taxon it contains. However, as is the case here, the topology of a phylogeny and the preference for clearly diagnosable groups may tip the balance in favour of monobasic taxa. In addition, higher-level taxa that are currently monobasic may well expand as new taxa are discovered and phylogenies become more refined.

The monophyly of the traditional Platygastroidea was found in all analyses. Therefore, we organized our evaluation of possible classification schemes with that group recognized at the family level. The sister group of platygastroids is a clade made up of *Nixonia* + *Neuroscelio* (Fig. 5). To our knowledge, there are no morphological characters that unite platygastroids and these two genera to the exclusion of other platygastroids, nor are there morphological character combinations that uniquely unite *Nixonia* and *Neuroscelio*. Therefore, we concluded that these two genera are best placed in their own families even though that means that, in terms of extant species, the two groups are monobasic. At least in the case of the Neuroscelionidae, two other fossil genera are known, *Brachyscelio* and *Cenomanoscelio*.

For the remainder of the platygastroids in the phylogenomic analysis two comparable classifications could be reasonably proposed. One option would be to recognize them all as the single-family Scelionidae. A second scheme would be to recognize the Sparasionidae and a restricted sense of the Scelionidae as separate families. We prefer the latter for several reasons. The restricted concept of Scelionidae corresponds to the main scelionid clade, a quite robust result that emerges from numerous analyses. The genera within Sparasionidae are charismatic (at least from our perspective), with well-defined, easily appreciated morphological characters that make the family readily identifiable. Recognizing the Sparasionidae as a family further reveals the relationship among its constituent genera. Although that relationship among ‘sparasionids’ would also be apparent by recognizing them as a subfamily of scelionids, none of the analyses so far have provided a robust hypothesis of relationships among all the genera in the main scelionid clade. We could recognize subfamilies such as Sparasioninae, Telenominae, Teleasinae, and perhaps Scelioninae (restricted to the genera included in the tribe Scelionini), but that leaves a very large number of genera unplaced at the level of subfamily. In separating them from the main scelionid clade, the monophyly of the sparasionids would not be lost amid the remaining confusion within a larger Scelionidae.

We also considered the possibility of including the genus *Archaeoteleia* in a monobasic family, sister to the remaining sparasionids. We opted not to do so because, unlike the case with *Nixonia* and *Neuroscelio*, we can articulate a set of easily observable morphological characters that *Archaeoteleia* shares with the other sparasionids. *Orwellium*, although originally described as a scelionid, consistently emerges as either the sister group of Platygastridae or as part of a basal trichotomy with other platygastroids. We propose, therefore, that it be included within the family Platygastridae. The task of dividing the platygastroids into subfamilies should await more comprehensive taxon sampling.

The final two families in the revised classification are represented in our analyses by only one genus each, *Janzenella* and *Huddlestonium*. Our treatment of them is made more difficult by the fact that they could not be included in the phylogenomic portion of the work, and the nodes at which they arise in the 4G and 4G + M studies do not have particularly strong bootstrap support values.

In our 4G + M analysis *Janzenella* is resolved as one part of a basal trichotomy that also includes platygastroids (with *Orwellium*) and *Neuroscelio*, and the ultrafast bootstrap support value for that node is 83%. We considered two options: either to recognize *Janzenella* as a separate, monobasic family or treat it as a platygastrid. The latter option would mean that there would be no combination of morphological synapomorphies or even diagnostic characters to recognize platygastroids. Therefore, despite our general desire to avoid monobasic taxa, we believe that the recognition of the family Janzenellidae is the best option. In the 4G and 4G + M results, *Huddlestonium* groups together with *Nixonia*. We view this with some suspicion as it is only represented by 18S and 28S sequences. Those data certainly support its placement near the root of Platygastroidea, but to conclude that it positively indicates a close relationship with *Nixonia* is, in our opinion, unwarranted. The genus, together with those that are morphologically similar and very likely related to it (see the family-level treatment for Geoscelionidae) is a morphological outlier in the Platygastroidea. Although they all possess the distinctive papillary sensilla on the ventral side of the female clava, these genera have no apparent laterotergites. The scarcity of specimens means that the details of the metasomal anatomy have not yet been worked out. We are unaware of any morphological synapomorphies that would unite these genera with any other platygastroid, and so we treat them here as the separate family Geoscelionidae.
An opposing argument may be that these two families would be better treated as genera incertae sedis, since we do not have strong evidence to indicate where they fit in the overall phylogeny. Although we are not certain of their position vis-à-vis the other clades in the backbone of the Platygastroidea, we have great confidence that neither Janzenella nor Huddlestonium (and its relatives) belong within any of the other families, nor can they be grouped together. We believe that it is our responsibility to put forth the strongest hypothesis that can be made on the basis of our results. Therefore, we have treated them as separate families in their own right.

In summary, we recognize eight families of Platygastroidea, seven of which are extant. The Proterosceliopsidae are known only from fossils. Two families – Nixoniidae and Janzenelliidae – are monobasic, but we believe that the evidence supporting their recognition at the rank of family is compelling. Two of the three genera of Neuroscelionidae are known only from fossils. The Geoscelionidae is an ancient lineage, today represented only by two exceedingly rare genera. The Sparasionidae are widespread, although they are notably absent from Australia. Finally, this schema revives the core of the traditional concepts of Scelionidae and Platygastroidea. We look forward to further advances that fresh collections will bring, as well as to insights into the internal phylogeny of platygastrids and scelionids.

Key to families of Platygastroidea

The vast majority of extant platygastroids that one is likely to encounter will be species of the families Platygastroidea, Scelionidae or Sparasionidae. As a general rule, platygastrids are minute, the antennae have no more than 10 segments, and the wing venation is reduced to a single tubular vein in the fore wing or is entirely absent. Sparasionids are generally much larger, have a tibial spur formula of 1-2-2 (these structures are large and clearly visible in this family), the antennae in both sexes are 12-merous, and they have a bulla in the fore wing at the apex of the submarginal vein. Scelionids are very diverse in size, shape, and sculpture, and no simple combination of characters is sufficient to separate every species from the other two families. They are probably most easily identified by a process of elimination. The greatest difficulty is likely to be encountered in the smallest scelionids in which much of the body sculpture and the wings have been greatly reduced or lost, and in which the number of antennal flagellomeres is reduced, often with a coalescence of the apical segments into an enlarged club (or clava) in the females. In the key, we use the common but morphologically imprecise term antennal segments. We recognize, though, that the antenna of these wasps has but three true segments. The radicle, at the proximal end of the scape, is not included in these counts.

1. Laterotergites absent, metasomal terga (T) and sterna (S) closely interlocked (Fig. 9A, B); body short and stout, coarsely sculptured (Fig. 7A, B); female antenna with 11–14 segments; extant species known from south-eastern Brazil, Venezuela and sub-Saharan Africa, very rare 
   – Laterotergites present, flexed ventrally to form a distinct submarginal ridge (lt; Fig. 9C) or broadly clasping the sterna (lt; Fig. 9D); body shape variable; female antenna with 7–15 segments

Fig. 9. (A) Huddlestonium exu Polaszek & Johnson (OSUC 148693), lateral view; (B) Plaumannion yepezi García (OSUC 146571), lateral view; (C) Dichoteleas sp. (USNMENT01197871), ventral view; (D) Fidiobia sp. (USNMENT01059802), ventrolateral view. Scale bars in millimetres. it2, laterotergite 2; it3, laterotergite 3.

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2. Mesepimeral sulcus absent (Fig. 10A); antenna with 10 fewer segments (11 in males of the Chilean endemic *Orwellium*); worldwide in distribution, very common ........................................... Equuleidae

- Mesepimeral sulcus usually present, indicated by a line of foveae parallel to mesopleural-metapleural suture (mees; Fig. 10B); if absent (*Aeneoscelio*), then antenna with 12 segments and gena with long, dense, whitish setae; number of antennal segments variable, ranging from 7–15 .................................................. 3

3. Antenna with 14 or 15 segments; metasomal segments with broad, paired depressions along anterior margin (arrows in Fig. 11A); pronotal cervical sulcus setose (prcs; Figs 10A, 11B) ........................................... 4

- Antenna with 12 or fewer segments; metasomal segments either simple (no foveae or depressions), or with line of foveae along anterior margins (Fig. 11C, D); pronotal cervical sulcus without setation ................................. 5

4. Marginal vein in fore wing (C+R) well developed (Fig. 12A); transepisternal line present (tel; Fig. 12C); malar sulcus present (mas; Fig. 12D); paired papillary sensilla on female clavomeres arranged in longitudinal

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**Fig. 10.** (A) *Isolia* sp. (OSUC 698060), lateral view; (B) *Dicroscelio* sp. (USNMENT01109621_4), lateral view. Scale bars in millimetres. Mees, mesepimeral sulcus.

**Fig. 11.** (A) *Nixonia watshami* Johnson & Masner (OSUC 188493), dorsal view; (B) *Nixonia stygica* Johnson & Masner (OSUC 146451), lateral view; (C) *Sparasion* sp. (CASENT 2133571), dorsal view; (D) *Probaryconus* sp. (USNMENT01109596), dorsal view. Scale bars in millimetres. Prcs, pronotal cervical sulcus.
Fig. 12. (A) *Proterosceliopsis tonquata* Talamas, Shih & Ren (CNU-HYM-MA 2016106), detail of fore wing venation; (B) *Nixonia pecki* Johnson & Masner (OSUC 146419), detail of fore wing venation; (C) *Aphanomerus* sp. (FBA047790), lateral view; (D) *Calliscelio* sp. (USNMENT00896490), anterior view; (E) *Lapitha* sp. (OSUC 170003), ventral view; (F) *Nixonia watshami* Johnson & Masner (OSUC 149432), ventral view. Scale bars in millimetres. *Mas*, malar sulcus; *ps*, papillary sensilla; *tel*, transepisternal line.

Fig. 13. (A) *Sparasion* sp. (CASENT 2136557), anterior view; (B) *Neuroscelio doddi* Galloway, Austin & Masner (OSUC 147252), anterior view. Scale bars in millimetres. *Pal*, labial palp.

pairs (*ps*; as in Fig. 12E); antenna 14- or 15-segmented; Cretaceous fossils .................. *Proterosceliopsidae*

- Fore wing without marginal vein (Fig. 12B); transepisternal line absent (Figs 10A, B, 11B); malar sulcus absent (as in Fig. 13A, B); paired papillary sensilla arranged transversely on female clavomeres (*ps*; Fig. 12F); antenna 14-segmented; extant; Afrotropical and Oriental regions ________________________________ *Nixoniidae*
5. Middle tibia with two apical spurs .......................... 6
   - Middle tibia with one apical spur ........................ 7

6. Fore wing with bulla, i.e., a gap between the apex of the submarginal vein and the more distal venation (Fig. 12A); metasomal segments 3–5 with a line of foveae along anterior margin (Figs 8D, 11C); maxillary palp elongate and easily visible, 5-segmented (pal; Fig. 13A); cosmopolitan, but excluding Australia .........................
   - Fore wing without bulla, submarginal vein continuous to costal margin apically (Fig. 7E); sutures between metasomal segments 3–5 simple, without line of foveae (Figs 7D, 11D); maxillary palp minute, 2-segmented (pal; Fig. 13B); Australia and southeast Asia ...............
   ............................................. Scelionidae

7. Body strongly depressed (Fig. 7F, G); marginal vein absent from fore wing (Figs 7F, 12B); antenna 11-segmented; malar sulcus absent (as in Fig. 13A, B); anterior margin of metasoma broadly rounded (arrow in Fig. 14A); extant species known only from Costa Rica ..................................................
   - Body shape quite variable, if strongly depressed, then fore wing with distinct marginal vein (C+R; as in Fig. 12A); antenna with 7–12 segments; malar sulcus present (mas; Fig. 12D); anterior margin of metasoma carinate (arrow in Fig. 14B); worldwide in distribution, very common ........................................ Scelionidae
   - Body strongly depressed (Fig. 7F, G); marginal vein absent from fore wing (Figs 7F, 12B); antenna 11-segmented; malar sulcus absent (as in Fig. 13A, B); anterior margin of metasoma broadly rounded (arrow in Fig. 14A); extant species known only from Costa Rica ..................................................

Table S1. Sequence and host information for taxa used in the analyses. Label data for all specimens are accessible at mbd-db.asc.ohio-state.edu.

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Author contributions
Huayan Chen and Zachary Lahey led the effort to generate molecular data and conduct all of the analyses. Additional molecular data were the result of work by Elijah J. Talamas, Alejandro A. Valerio, Hans Klompen and Andrew Polaszek. Morphological data were largely generated by Ovidiu A. Popovici, Elijah J. Talamas and Norman F. Johnson. All authors contributed to the interpretation of the results. Writing of the manuscript was primarily conducted by Norman F. Johnson, Huayan Chen and Zachary Lahey. The project was conceived and directed by Andrew D. Austin and Norman F. Johnson.

Supporting Information
Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Morphological characters and character states used in the phylogenetic analysis; supplemental figs S1–S28; References Cited in Supporting Information.
Data availability statement

The data that support the findings of this study are openly available in Dryad at http://doi.org/dryad.k0p2ngf72.

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