

Evolving perspectives in Hymenoptera systematics: Bridging fossils and genomes across time

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Abstract

The recent advances in sequencing technologies, phylogenomics and divergence dating methods call for an integrative review of the current state of Hymenoptera systematics. We here explore the impact of these latest developments on the Hymenoptera phylogeny and our understanding of the timing of Hymenoptera evolution, while identifying the current methodological constraints and persistent knowledge gaps that warrant further investigation. Our review highlights the lack of consensus among the backbone phylogeny of Hymenoptera between key phylogenomic studies, as the higher level phylogeny remains unresolved in key nodes such as the relationships among Eusymphyta, the relationships within the Infraorder Proctotrupomorpha and the placements of the superfamilies Ichneumonoidea, Ceraphronoidea and Vespoidea. Furthermore, we underline the huge variation in divergence age estimates for Hymenoptera and detect several major gaps and/or disagreements between the fossil record and available age estimates, either due to the poorly studied fossil record or problematic age estimates, or both. To better understand the timing of Hymenoptera evolution and the role of key diversification factors, we will need continuous efforts to (i) reconcile conflicts among morphological and molecular phylogenies, by improving taxon sampling of underrepresented lineages, applying novel techniques to study morphology, making use of genome-scale data and critically assessing incongruences in genetic markers; (ii) improve the Hymenoptera fossil record, by exercising integrative taxonomy and bringing together paleontologists and neontologists; and (iii) reconcile age estimates, by relying on tip dating approaches to bridge fossils, morphology and genomes across time.

KEYWORDS

divergence dating, literature review, phylogenetic methods, phylogenomics, taxonomy

INTRODUCTION

Hymenoptera, encompassing sawflies, wasps, ants and bees, stands out as one of the most diverse organism groups on Earth. With over 154,000 identified species (Aguiar et al., 2013; Huber, 2017; van Noort & Broad, 2024) and potentially up to 2.5 million yet-to-be-

described species in existence (Forbes et al., 2018; Stork, 1997; Ulrich, 1999), Hymenoptera plays a pivotal role in nearly all terrestrial ecosystems. Furthermore, these insects hold significant economic value, serving as parasitoids, predators and pollinators (Austin & Dowton, 2000; Huber, 2017; Polaszek & Vilhelmsen, 2023; van Noort & Broad, 2024).

Some of the most interesting and ongoing research questions on Hymenoptera concern the evolution and shifts in their lifestyles,

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which may have contributed to the diversification across the order. The earliest lineages of Hymenoptera, sawflies (suborder Symphyta), predominantly exhibit phytophagy, with the evolution of parasitoidism likely occurring only once within Hymenoptera. This transition likely took place within the common ancestor of the symphytan Orussoidea and wasps, bees and ants (suborder Apocrita) (Blaimer et al., 2023; Polaszek & Vilhelmsen, 2023; Vilhelmsen et al., 2024). This first parasitoid was likely an idiobiont targeting wood-boring beetle larvae, using a simple strategy of immobilizing their host at an early stage of development and preventing further growth or development of the host. From this modest origin, a remarkable diversification ensued, leading to a variety of lifestyles, including koinobiont parasitism, hyperparasitoidism, kleptoparasitism/parasitoidism, incorporation of polydnviruses and predatory nest provisioning (Polaszek & Vilhelmsen, 2023; van Noort & Broad, 2024). Conversely, several lineages within Apocrita have subsequently reverted to phytophagy, representing a potential key innovation for the overall diversification of the group, as well as influencing the evolution of eusociality (Blaimer et al., 2023).

Our understanding of these remarkable evolutionary patterns is highly dependent on a resolved and time-calibrated phylogeny of Hymenoptera. Rasnitsyn (1988) proposed one of the first classifications of Hymenoptera, and various aspects of this classification are still accepted today. This includes Symphyta being a paraphyletic grade with respect to Apocrita, and a single presumed origin of parasitoidism during the evolution of Hymenoptera, with the parasitoid symphytan superfamily Orussoidea consistently found as the sister group to Apocrita. Rasnitsyn (1988) also divided Apocrita into four Infraorders: Ichneumonomorpha (Ichneumonoidea), Proctotrupomorpha (Cynipoidea, Platygastroidea, Chalcidoidea, Mymarommatoidea and Proctotrupeoidea, and Diaprioidea), Evaniomorpha (Evanioidea, Trigonoidea, Ceraphronoidea, Stephanoidea and Megalyroidea) and Vespomorpha (Aculeata), all of which are still used regularly. A series of phylogenetic studies using morphological, molecular (ribosomal, mitochondrial and nuclear loci) and combined datasets were published in the early 2010s as part of the Hymenoptera Tree of Life Project, greatly improving our understanding of the higher level relationships of Hymenoptera (e.g., Heraty et al., 2011; Klopstein et al., 2013; Schulmeister, 2003; Sharkey et al., 2012; Vilhelmsen, 2001; Vilhelmsen et al., 2010). Sharkey (2007) provided the last comprehensive overview of the higher level phylogeny and classification of Hymenoptera, in which he recognized Diaprioidea as a distinct superfamily. The total number of superfamilies ranged from 20 to 27, with 89–132 families recognized in the literature (Aguiar et al., 2013; Goulet & Huber, 1993; Sharkey, 2007). At the time of writing this paper (April 2024), 29 superfamilies and 143 extant families are recognized in light of recent taxonomic changes, most notably within Proctotrupomorpha and Aculeata (Figure 1 and Table S1a). In addition, six additional extinct superfamilies and around 67 more extinct families are currently recognized (Table S1b).

The history of insect phylogenetics has been reviewed extensively in the literature (e.g., Kjer et al., 2016; Tihelka et al., 2021; Wipfler et al., 2016; Young & Gillung, 2020; Zhang et al., 2019),

including studies focusing more on specific lineages of Hymenoptera (e.g., Borowiec, Moreau, & Rabeling, 2021; Danforth et al., 2013; Polaszek & Vilhelmsen, 2023; Sharkey, 2007; van Noort & Broad, 2024). For this review, we chose to focus mostly on the recent advances in Hymenoptera phylogenomics and evolutionary research starting around 2014; we found that around this pivotal time, the use of second-generation/massively parallel sequencing found broad adoption in the community, allowing the generation of large quantities of genetic markers in comparison with traditional Sanger sequencing (from here on referred to as multilocus) across various lineages of Hymenoptera.

In parallel, the field of divergence time estimation has been developing rapidly, powered by phylogenomic advances that keep providing more robust phylogenies, new bioinformatic tools and mathematical algorithms that allow for more complex evolutionary models, and greater emphasis on the fossil record, which is providing increasingly reliable and older evidence for calibrating phylogenies (reviewed extensively in Donoghue & Yang, 2016; Guindon, 2020; López-Antoñanzas et al., 2022; O'Reilly et al., 2015; Wright et al., 2022). As a result, there are dozens of dating studies on Hymenoptera using different dating approaches, aiming at inferring the timing of origin of lineages at different taxonomic levels and understanding diversification patterns and speciation drivers in this megadiverse order, but these have never been reviewed systematically.

We start this review by providing an overview of both phylogenomic and divergence dating methods and their application in Hymenoptera. Thereafter, we give a detailed review of the major taxonomic changes in the higher phylogeny and classification across Hymenoptera, in light of phylogenomic data and divergence age estimates. Finally, we discuss the prospects and challenges for resolving the phylogeny of Hymenoptera and improving age estimates, and summarize open questions in Hymenoptera systematics and evolution.

OVERVIEW OF PHYLOGENOMIC METHODS

Mitochondrial genomes have been among the first to be sequenced given the relative ease of data acquisition and have often been published in single-species contributions, eventually leading to larger datasets examining patterns across superfamilies (e.g., Menezes et al., 2024; Tang et al., 2019; Zheng et al., 2022; Zhu et al., 2023). This approach is further expanded with the ability to extract mitogenomic data from sequence data acquired through targeted enrichment approaches (Allio et al., 2020), which can provide complementary data to the nuclear loci that were the primary targets. However, mitochondrial datasets can sometimes lead to contradictory results to those of their nuclear counterparts. This mitochondrial vs nuclear discordance can be the result of a combination of factors, including high levels of substitution saturation, elevated Adenine/Thymine (AT) content, nuclear mitochondrial DNA segments, or *Wolbachia* (Allio et al., 2020). Menezes et al. (2024) have shown that certain mitochondrial genes (*COI*, *16S*, *NAD5* and *NAD2*) perform better than others (*ATP6*, *COII*

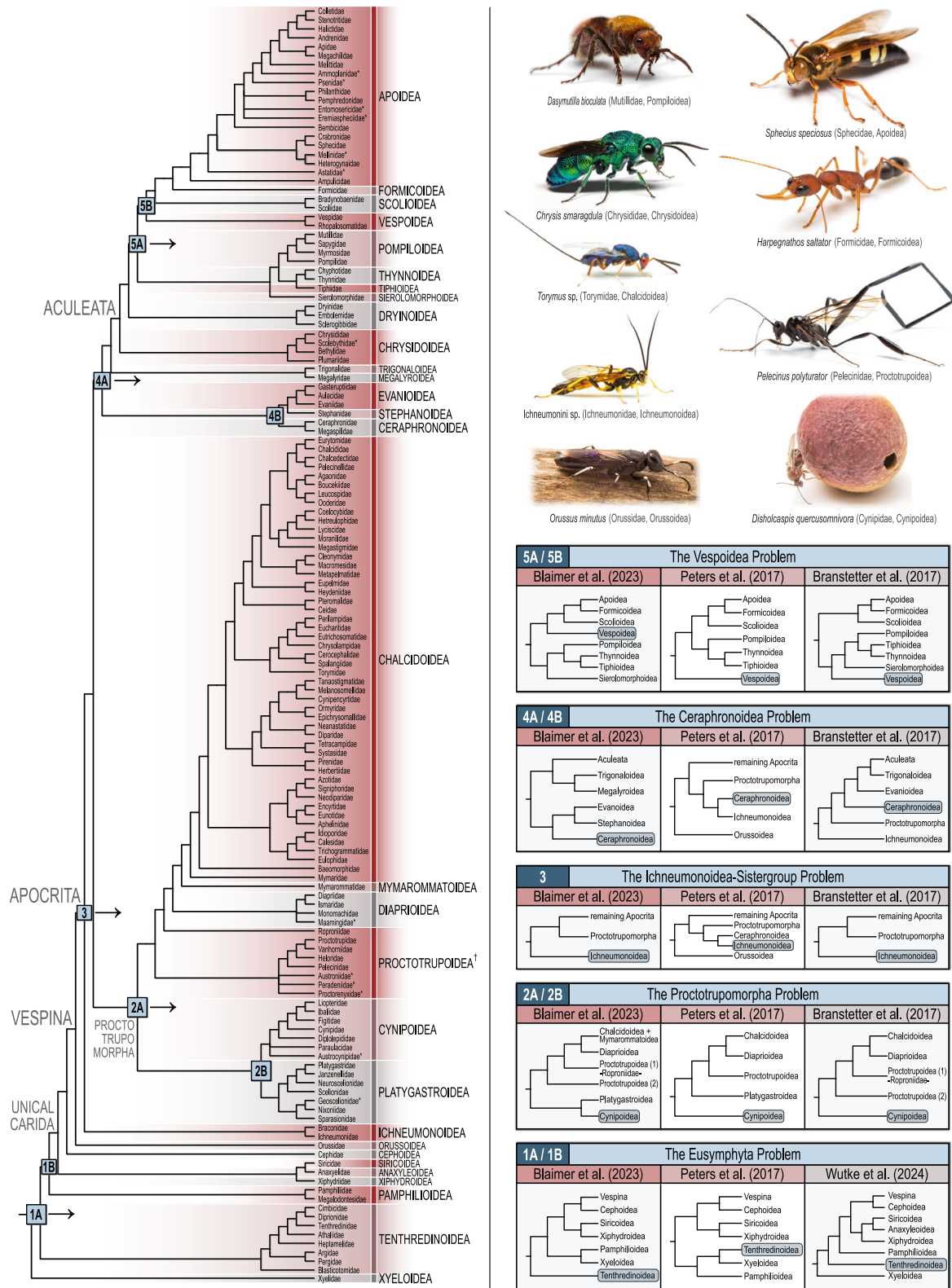


FIGURE 1 Summary of the phylogenetic relationships of Hymenoptera, represented by 143 extant families. The phylogeny follows the preferred analysis of Blaimer et al. (2023; C-1 topology) except for Chalcidoidea and Symphyta. The phylogeny of Chalcidoidea follows the topology and taxonomy of Cruaud et al. (2024) and the Symphyta follow Wutke et al. (2024). Taxa marked with asterisks have been grafted onto the phylogeny based on findings from other studies. The superfamily Proctotrupomorpha is indicated with a dagger because of the inferred paraphyly with respect to Roproniidae. The newly recognized apoid families Entomosericidae and Eremiasphecidae have been grafted onto the tree with unresolved phylogenetic position. All photos by Y. Miles Zhang.

and 12S) in recovering a concordant relationship with nuclear markers within Vespidae, but whether this pattern holds across Hymenoptera is unknown.

The first published phylogenomic studies of Hymenoptera using nuclear genes mainly utilized transcriptomes (Johnson et al., 2013; Peters et al., 2017). This is largely due to the 1KITE (1K Insect Transcriptome Evolution) project, which led to the seminal Misof et al. (2014) study of insect phylogenomics, in which Hymenoptera was recovered as the sister group to the remaining Holometabola. Subsequent 1KITE projects include a targeted study on Hymenoptera (Peters et al., 2017), and studies with a broader sampling of specific groups including Apoidea (Sann et al., 2018, 2021) and Chalcidoidea (Peters et al., 2018; Zhang, Lindsey, et al., 2020). However, one major limitation of transcriptomic studies is that only fresh specimens can be used, as RNA degrades rapidly, thus often limiting the breadth of taxonomic sampling to common or easily obtained species.

One major advantage of targeted capture methods such as anchored hybrid enrichment (AHE, Lemmon et al., 2012) or sequencing ultraconserved elements (UCEs, Faircloth et al., 2012) over transcriptomics is the ability to recover data from older specimens, a field which is sometimes referred to as ‘museomics’. This advancement allowed for more active use of the vast entomological collections from natural history museums, which often house rare or even extinct/extirpated taxa to be included in phylogenomic studies. A few studies have used different targeted capture methods on groups such as Vespidae (Bank et al., 2017; Piekarski et al., 2018), Chalcidoidea (Baker et al., 2020; Maletti et al., 2021; Zhang, Heraty, et al., 2022), Ichneumonoidea (Klopfstein et al., 2019; Sharanowski et al., 2021) and Apoidea (Sann et al., 2018), whereas the majority of recent phylogenomic studies on Hymenoptera utilized UCEs (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Faircloth et al., 2015). Unlike the other targeted capture methods mentioned above which exclusively focus on protein-coding genes and generally target <1000 loci, the widely used HymenopteraV2 UCE probes target >2500 loci and include both exonic and intronic regions (Bossert & Danforth, 2018; Zhang et al., 2019). The target capture method, particularly UCE phylogenomics, offers notable advantages in its ability to sequence hundreds of loci from a single, non-destructively extracted, minuscule dried specimen with exceedingly low DNA yield (e.g., Trichogrammatidae or Mymaridae, which can measure less than 0.5 mm in length and yield less <1–5 ng of DNA), especially when combined with techniques such as whole-genome amplification (Cruaud et al., 2018, 2019). This presents several significant implications: (1) Utilizing a single specimen mitigates the risk of potential contamination that may arise when sequencing multiple specimens from distinct cryptic or closely related species; (2) enabling the use of historical specimens, some over a century old, with severely degraded DNA and occasionally representing rare lineages that have only been collected a few times; and (3) facilitating the vouchering of the extracted specimen, thus allowing for subsequent re-examination for error-checking purposes and/or for taxonomic studies. Additionally, the accompanying, regularly updated open-source pipeline Phyluce (Faircloth, 2016) allows the inclusion of UCE sequence data from various sources. To this end,

genomes, transcriptomes and target-enriched UCE loci can be combined in one analysis (Bossert et al., 2019; Kieran et al., 2019; Kulkarni et al., 2021). Finally, the currently used, improved Hymenoptera V2 UCE bait sets were developed with downward compatibility in mind: Branstetter, Longino, et al. (2017) incorporated additional genomes for the bait design, thus increasing the number of loci captured, yet also assuring overlapping loci with the initial Hymenoptera V1 bait set. This has led to an exponential increase of large-scale phylogenomic research on Ichneumonoidea (e.g., Jasso-Martínez et al., 2022; Santos et al., 2019, 2021, 2022), Chalcidoidea (e.g., Cruaud et al., 2021, 2024; Rasplus et al., 2020), Cynipoidea (e.g., Blaimer et al., 2020; Ward et al., 2022, 2024; Zhang, Buffington, et al., 2020), Apoidea and especially bees (e.g., Bossert et al., 2022; Sless et al., 2022), or Formicoidea (e.g., Blaimer et al., 2018; Borowiec, 2019; Branstetter, Longino, et al., 2017). The Blaimer et al. (2023) study stands out as the taxon-densest time-calibrated phylogeny of Hymenoptera to date (765 taxa in ~120 currently recognized families), delving into the origins of crucial innovations that may have led to the significant diversity of the order Hymenoptera that we see today. Surprisingly, among the four traits examined—1. wasp waist of Apocrita, 2. stinger of Aculeata, 3. parasitoidism and 4. secondary phytophagy—transitions to secondary phytophagy (reverting from parasitoidism) emerged as a significant factor influencing the diversification rate in Hymenoptera.

BRIEF HISTORY OF DIVERGENCE DATING

The fossil record is the first and essential evidence for reconstructing the evolutionary history of life. Rasnitsyn (1988) provided one of the first timetrees for Hymenoptera based solely on the comprehensive fossil record at the time, with the presence of the first undisputed Hymenoptera in the Middle to Late Triassic. Further, he concluded that around half of the superfamilies occurred during the Jurassic and most of the extant families during the Early Cretaceous (Rasnitsyn, 1988; Rasnitsyn & Quicke, 2002). The very patchy nature of the fossil record is also depicted, with the record of several families having long gaps spanning tens of millions of years. These time trees presented a significant advance at the time, however, they must be understood as minimum age estimates for the origin of Hymenoptera families. This is due to both temporal and spatial bias in the fossil record, which implies that the earliest known fossils are almost certainly younger than the first living members of the families. Meanwhile, some of the methods for establishing maximum ages based on the fossil record have been proposed, which take into account fossil richness, average paleontological species duration and preservation potential (Marshall, 2019), but none of which has to our knowledge been applied to Hymenoptera yet.

The establishment of the molecular clock hypothesis, which suggests the correlation of molecular rates of evolution and time, has led to the development of various parametric approaches for divergence time estimation based on molecular data, as well as the semiparametric penalized likelihood method (Paradis, 2013; Sanderson, 2002).

The latter, for example, has been applied in Ichneumonoidea for dating the origin of bracoviruses (Whitfield, 2002) and microgastroid wasps (Murphy et al., 2008). These approaches have quickly been replaced by Bayesian methods and specifically the node dating approach, where fossils are used to calibrate the molecular clock, thereby providing a hard minimum age for the node to which they are assigned to. This approach allows for estimating the uncertainty in the obtained divergence dates, and thus also provides maximum age estimates for nodes. The majority of dating studies in Hymenoptera (around 70%) apply a node-dating approach to calibrate the molecular clock (e.g., Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Cardinal & Danforth, 2013; Niu et al., 2022; Nyman et al., 2019; Peters et al., 2017; Sann et al., 2018; Tang et al., 2019). However, several conceptual concerns have been raised about node dating. Specifically, three major limitations of node dating have been discussed in the literature: (1) node dating cannot consider uncertainty in the interpretation of fossils and its phylogenetic placement, (2) it requires setting a node age prior where the choice of the shape and maximum of the prior distribution is essentially arbitrary and (3) there might be interactions between the node and tree age priors (Ho & Phillips, 2009; Ronquist et al., 2012).

As a response to the observed issues of the node dating strategy, so-called tip dating approaches have been developed, where fossils are treated as tips of a phylogeny (Pyron, 2011; Ronquist et al., 2012). Their placement can either be inferred using morphological data, that is, total-evidence tip dating (Ronquist et al., 2012), or it can be constrained to a clade to account for uncertainty in the fossil placement, that is, tip dating under the unresolved Fossilized Birth-Death (FBD) tree prior (Heath et al., 2014). The FBD prior considers that diversification processes (speciation and extinction) give rise to phylogenies and explicitly incorporates the fossilization process into the model (Heath et al., 2014). Subsequently, various extensions to the tip dating approach under the FBD prior have been developed (e.g., Gavryushkina et al., 2014; Zhang et al., 2016, 2023). Interestingly, since the seminal total-evidence tip dating study by Ronquist et al. (2012) on Hymenoptera, the order has become a model group for testing the performance of the newly developed FBD models, allowing us to assess model-dependent variation in the age estimates for Hymenoptera (Zhang et al., 2016, 2023). Next to these studies, there have been only a handful of tip dating studies on lower taxonomic levels, concerning Apoidea (Almeida et al., 2023; Bossert et al., 2022; Gonzalez et al., 2019), Chrysididae (Lucena & Almeida, 2022), Evanioidea (Jouault et al., 2022), Ichneumonidae (Santos et al., 2022; Spasojevic et al., 2021) and Stephanidae (Ge et al., 2023).

REVIEW OF MAJOR TAXONOMIC CHANGES AND DATE ESTIMATES

In this section we provide a review of major phylogenetic/genomics studies across Hymenoptera from ~2014 on and their implications for the systematics of the group, with a particular focus on three large-

scale studies using either transcriptomes (Peters et al., 2017) or UCEs (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017). Names for informal higher groupings such as Proctotrupomorpha and Evanioomorpha, along with valid superfamilies and families also follow these three studies. Our phylogeny (Figures 1 and 2) largely follows Blaimer et al. (2023) as it is the taxon-densest study to date, while certain family-level relationships are further fine-tuned based on studies that focus on the respective groups (Boudinot et al., 2022; Chen et al., 2021; Cruaud et al., 2024; Hearn et al., 2024; Malm & Nyman, 2015; Niu et al., 2022; Sann et al., 2018, 2021).

We also review divergence age estimates for the major higher groupings within Hymenoptera (suborders, superfamilies and families) and mention some example studies on lower taxonomic levels. For this purpose, we compiled an exhaustive list of dating studies on Hymenoptera and therein reported divergence age estimates and confidence intervals (Table S2). If not stated otherwise, the age estimates reported in the main text below are derived from node dating studies and represent either mean or median estimates for crown-groups. Moreover, for each taxon, we only discuss the estimates from studies specifically aiming at inferring the age of that taxon, thus omitting studies with inappropriate sampling of the target taxon. For superfamilies, we mention estimates from studies focusing on the higher level relationships of Hymenoptera if they included more than one taxon for a superfamily and if the sampling was not restricted to a couple of recently diverged taxa. If several sensitivity analyses were performed in a dating study, we here reported the estimates from the preferred analysis only, which was either labelled as such by the authors of the study or inferred by us from the text of the study. Finally, we compare the current age estimates to the fossil record of Hymenoptera, which we compiled from the Paleobiology Database (PaleoBioDB; accessed on 4 January 2024) and relevant literature (Table S3a–c). In the main text of the manuscript, the age of fossils and relevant compression and amber deposits is given as a mean of the minimum and maximum age reported in the Paleobiology Database, except for Baltic amber, where we gave a conservative range of 48–34 Ma due to the large uncertainty in the age of the amber (but see Sadowski et al., 2017, 2020).

Hymenoptera

Our comprehension of the evolutionary relationships within Hymenoptera is expanding rapidly, resulting in significant advancements from large-scale phylogenomic studies (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Peters et al., 2017). Despite the substantial improvement in taxa and locus sampling, certain pivotal relationships among Hymenoptera remain controversial and warrant attention as notable challenges (Figure 1).

1. The Eusymphyta problem: The relationships among the most ancient lineages of Hymenoptera, particularly within Eusymphyta (Pamphilioidea, Xyeloidea, Tenthredinoidea), are unresolved. The question of whether Eusymphyta forms a monophyletic group

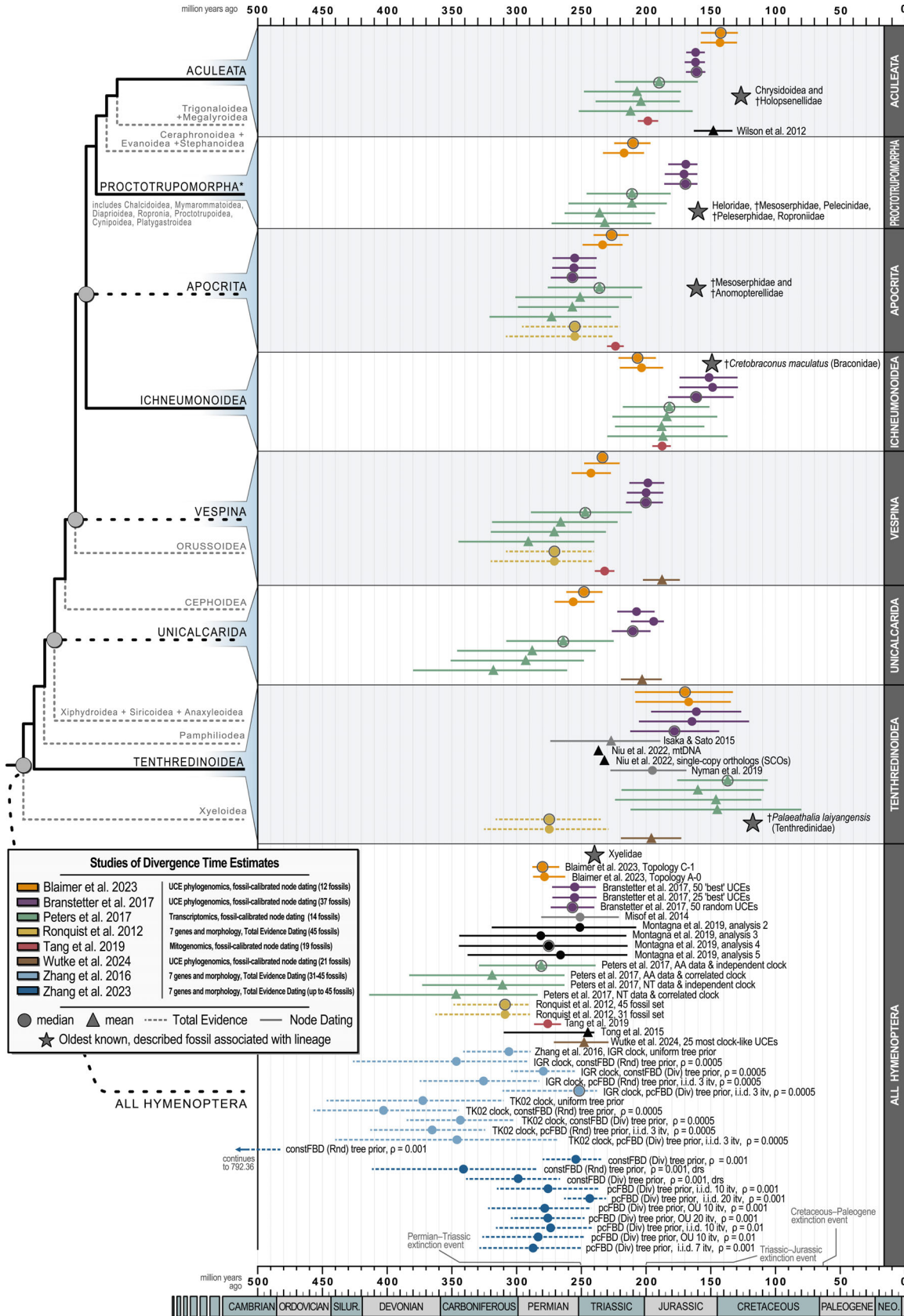


FIGURE 2 Legend on next page.

- (Peters et al., 2017) or represents an evolutionary grade, with Xyeloidea (Wutke et al., 2024) or Tenthredinoidea (Blaimer et al., 2023) as the earliest branching lineage, demands further investigation (Figure 1, inset 1A/1B). Wutke et al. (2024) demonstrated that the inclusion of distantly related, non-Hymenopteran outgroups can drastically change the ingroup topology of the symphytans, whereas inferring the likely root position using a non-reversible Markov model could circumvent this problem. Using the latter approach, they have consistently recovered Xyelidae as the most ancient lineage of Hymenoptera (Wutke et al., 2024). This position of Xyelidae is also in agreement with both the most comprehensive morphological studies (Beutel & Vilhelmsen, 2007; Schulmeister, 2003; Vilhelmsen, 2001) and paleontological evidence, as Xyelidae appear well before any other symphytans, including Tenthredinoidea, in the fossil record (Table S3b,c).
2. The Proctotrupomorpha problem: The position of the superfamily Cynipoidea within Proctotrupomorpha remains unresolved, with conflicting hypotheses suggesting it either as the sister to all other Proctotrupomorpha using transcriptome data (Peters et al., 2017), or forming a clade with Platygastroidea and both as the sister group to other Proctotrupomorpha in some multilocus, total-evidence and UCE studies (Blaimer et al., 2023; Klopstein et al., 2013) (Figure 1, inset 2A/2B). Additionally, Roproniidae renders Proctotrupeoidea paraphyletic in the two UCE studies (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017), despite its placement within the superfamily in earlier molecular works (Heraty et al., 2011; Klopstein et al., 2013). The morphological evidence is also inconclusive regarding the relationships among superfamilies of Proctotrupomorpha. A sister relationship of Cynipoidea + Platygastroidea has only been occasionally and weakly supported, often with homoplastic characters (Sharkey et al., 2012), while there has been more convincing but also disputable morphological evidence for a close relationship of Cynipoidea with Diapriidae, Platygastroidea and Proctotrupeoidea (Vilhelmsen et al., 2010). Ultrastructural characteristics of the spermatozoa support exclusion of Cynipoidea from Proctotrupomorpha (Lino-Neto & Dolder, 2001), while the ovipositor morphology (i.e., non-overlapping lower valves) separates both Cynipoidea and three Proctotrupeoidea families (Heloridae, Pelecinidae and Roproniidae) from the remaining Proctotrupomorpha (Quicke et al., 1994). Looking at the fossil record, Proctotrupeoidea is by far the oldest superfamily of Proctotrupomorpha, with fossil representatives of three extant families (Heloridae, Pelecinidae and Roproniidae) occurring already during the Middle to Late Jurassic (Shih et al., 2009, 2011). Thus, the fossil record rather supports the molecular phylogenies that recovered Cynipoidea and Platygastroidea as sister to Proctotrupeoidea plus the remaining Proctotrupomorpha.
 3. The Ichneumonoidea sister group problem: The placement of the superfamily Ichneumonoidea has always been unstable, being recovered either as the sister to Proctotrupomorpha in a four-gene analysis (Heraty et al., 2011), or as sister to the rest of Apocrita + Orussoidea in a study which expanded on the Heraty et al. (2011) study by adding three additional nuclear loci (Klopstein et al., 2013). This uncertainty is also reflected in the phylogenomic data, with Ichneumonoidea being sometimes recovered as the sister to the rest of Apocrita excluding Orussoidea (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017). Alternatively, Ichneumonoidea has also been recovered as the sister group to Ceraphronoidea, resulting in a monophyletic 'Parasitoida' clade alongside Proctotrupomorpha (Blaimer et al., 2023; Peters et al., 2017) (Figure 1, inset 3). This uncertainty affects our interpretation of which lineage represents the earliest apocritan parasitoids. The morphological analyses were either inconclusive regarding the position of Ichneumonoidea (e.g., Sharkey & Roy, 2002) or they recovered the superfamily as the sister group to Aculeata (e.g., Ronquist et al., 1999; Vilhelmsen et al., 2010)—a relationship supported by what has been interpreted as unconvincing morphological evidence and refuted by most molecular studies.
 4. The Ceraphronoidea problem: Tied to the Ichneumonoidea sister group problem above, the positioning of Ceraphronoidea is contentious, with hypotheses placing it either as the sister to Ichneumonoidea (Blaimer et al., 2023; Peters et al., 2017) or as part of Evaniomorpha *sensu lato* (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Heraty et al., 2011; Klopstein et al., 2013) (Figure 1, inset 4A/4B). Morphological analyses recovered Ceraphronoidea either nested within Proctotrupomorpha (Ronquist et al., 1999; Sharkey & Roy, 2002) or as a sister group to Megalynoidea and close to other traditional Evaniomorpha (Vilhelmsen et al., 2010), while there has been no clear morphological evidence for a sister relationship of Ichneumonoidea and Ceraphronoidea.
 5. The Vespoidea problem: The placement of superfamily Vespoidea within Aculeata presents another puzzle, with conflicting results suggesting it either as the sister to the rest of Aculeata using transcriptome data (Peters et al., 2017), or as the sister group to some major lineages within Aculeata based on total-evidence, multilocus and UCE data (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Klopstein et al., 2013; Sharkey et al., 2012) (Figure 1, inset 5A/5B). The morphological studies have failed to recover a monophyletic Vespoidea *sensu* Pilgrim et al. (2008) (Brothers, 1999; Ronquist et al., 1999; Sharkey et al., 2012) and thus provide no support for any of the recovered placement of Vespoidea within Aculeata in molecular studies.

FIGURE 2 Select divergence time estimates of crown-group Hymenoptera and higher level clades within the order. The phylogeny follows Blaimer et al. (2023), except for the phylogeny of Symphyta, which follows Wutke et al. (2024). Black dashed lines leading to Hymenoptera, Apocrita, Vespina and Unicalcarida are not part of the phylogenetic tree but indicate higher level groupings at the respective nodes. The median divergence times of Ronquist et al. (2012) are identical within individual groups and correspond to the divergences of their figure S2 (see 10.5061/dryad.j2r64). Further explanation for alternative dating analyses in each study can be found in original publications. For a compilation of Hymenoptera divergence times see Table S2. A comprehensive list of Hymenoptera fossils, including potential stem-group representatives, can be found in Table S3.

The reported age estimates from molecular dating studies for crown-group Hymenoptera range from the Early Mississippian in the Carboniferous (~350 million years, from here on abbreviated as Ma; excluding significantly older and clearly unrealistic estimates) (Zhang et al., 2016, 2023) to the Middle Triassic (~240) (Misof et al., 2014; Tong et al., 2015; Wutke et al., 2024), depending on the time divergence estimation method, model parameter settings, choice of the calibration points and the way the sampling of extant taxa is modelled (Blaimer et al., 2023; Misof et al., 2014; Peters et al., 2017; Ronquist et al., 2012; Tong et al., 2015; Zhang et al., 2016, 2023) (Figure 2 and Table S2). While the youngest of the age estimates (coming from studies aimed at dating a comprehensive insect phylogeny) would satisfy the hypothesis of co-diversification of Hymenoptera and angiosperms during the Cretaceous (Barba-Montoya et al., 2018; Coiro et al., 2019; Magallón et al., 2015; Ramírez-Barahona et al., 2020), the younger dates are very close to the age of the oldest undisputed Hymenoptera fossils, which are likely members of the family Xyelidae (242–237 Ma, Middle Triassic) (Kopylov, 2014; Rasnitsyn, 1964, 1969). This leaves little to no space for the discovery of older fossils, which is incompatible with the widespread distribution of Xyelidae already during the Middle to Late Triassic, ranging from Argentina (Lara et al., 2014) to South Africa (Schlüter, 2000), Europe (undescribed; Montagna et al., 2024), Middle Asia (Kopylov, 2014; Rasnitsyn, 1964, 1969), Japan (Oyama & Maeda, 2020) and Australia (Engel, 2005; Riek, 1955). Instead, the fossil record implies that the family and, thus, also the crown-group Hymenoptera must have originated earlier, possibly just after or even before the Permian–Triassic mass extinction event (~252 Ma). On the other hand, the oldest age estimates suggest the existence of long ghost lineages, sometimes spanning more than 100 Ma, which has been deemed unlikely by some authors (Zhang et al., 2016, 2023). The two most recent dating efforts on Hymenoptera, one based on node dating of the most comprehensive phylogeny of Hymenoptera to date (Blaimer et al., 2023) and the other aiming to reconcile age estimates for Hymenoptera within the total-evidence dating framework (Zhang et al., 2023), seem to converge on age estimates of ~280 Ma (mid- to early Permian) for the origin of the crown-group Hymenoptera. These estimates are also in agreement with the recent recalibration of the Misof et al. (2014) insect phylogeny following the discovery of several key insect fossils from the Early Triassic Monte San Giorgio Formation (~240 Ma) (Montagna et al., 2019). Despite this convergence of the latest studies, the age of the crown-group Hymenoptera should still be scrutinized, given the considerable confidence intervals around the estimates of Montagna et al. (2019), sensitivity of node dating studies to taxon sampling and calibration points, and complexity of total-evidence tip dating analyses coupled with our poor knowledge of Hymenoptera diversity (see below).

Symphyta

The monophyly and placement of the ancient superfamily Xyeloidea have been historically controversial. The superfamily consists of a

single family Xyelidae and two subfamilies (Xyelinae and Macroxyelinae), either being monophyletic or paraphyletic with respect to the remaining Hymenoptera, depending on the data type and analyses used (Heraty et al., 2011; Rasnitsyn, 1988; Schulmeister et al., 2002, 2003; Sharkey et al., 2012). All published phylogenomic studies to date that have included both subfamilies have shown Xyeloidea to be monophyletic (Niu et al., 2022; Wutke et al., 2024). Xyeloidea, Pamphilioidea and Tenthredinoidea were recovered as a monophyletic group (= 'Eusymphyta') by Peters et al. (2017) using transcriptome data. Branstetter, Danforth, et al. (2017) recovered a relationship of Xyeloidea, followed by Pamphilioidea, and then Tenthredinoidea as the sister to the rest of Hymenoptera (Unicalcarida); however, they did not include non-Hymenoptera outgroups and instead rooted the tree on Xyelidae. Blaimer et al. (2023), which also used UCE data but with non-Hymenoptera outgroups, did not recover a monophyletic Eusymphyta similar to Branstetter, Danforth, et al. (2017). However, in their study, it is the superfamily Tenthredinoidea that was the sister to the remaining Hymenoptera (Figure 1, inset 1A/1B). A newly published study focusing on Symphyta using UCEs included all extant symphytan families and recovered Xyeloidea as sister to the rest of Hymenoptera, followed by Tenthredinoidea + (Pamphilioidea + Unicalcarida) in their preferred tree not including outgroups (Wutke et al., 2024; Figure 1 inset 1A/1B). However, alternative relationships within the same Wutke et al. (2024) study also recovered different combinations between Xyelidae, Pamphilioidea and Tenthredinoidea when non-Hymenoptera outgroups were included, which could contribute reconstruction artefacts stemming from both very long branches connecting Hymenoptera to the outgroups, and the short internodes between the early branching superfamilies. Within Tenthredinoidea, Athaliidae and Heptamelidae are now recognized as distinct families, while Zenarginae is not supported as a distinct family (Malm & Nyman, 2015; Niu et al., 2022; Wutke et al., 2024). The superfamilies Siricoidea and Cephoidea remained strongly supported in all studies, and the enigmatic parasitoid superfamily Orussoidea is consistently recovered as the sister group to the remaining Apocrita, a grouping referred to as Vespina, to mark the beginning of parasitoidism within Hymenoptera (Blaimer et al., 2023; Peters et al., 2017; Wutke et al., 2024).

Symphytans received substantial attention in the context of divergence time estimation, with two main studies focusing on the suborder as a whole (Nyman et al., 2019; Wutke et al., 2024). The reported ages for Tenthredinoidea vary considerably, from the Late Triassic (~235 Ma) (Niu et al., 2022), over most of the Jurassic (195–170 Ma) (Blaimer et al., 2023; Isaka & Sato, 2015; Nyman et al., 2019; Wutke et al., 2024) to the Early Cretaceous (137 Ma) (Peters et al., 2017), depending on the taxon sampling, choice of calibration points and the inferred position of Tenthredinoidea relative to the other sawfly lineages. Regarding the remaining symphytan superfamilies, the age of crown-group Pamphilioidea has been estimated to the Middle Jurassic (174–165 Ma), Orussoidea (i.e., Orussidae) to the Late Cretaceous–Paleocene (69–64 Ma), Siricoidea (i.e., Siricidae) to the Late Cretaceous–early Eocene (68–54 Ma), Xiphidriidea (i.e., Xiphidriidae) to the late Eocene (37–33 Ma) and of Cephoidea

(i.e., Cephidae) to the Oligocene (31 Ma) (Nyman et al., 2019; Wutke et al., 2024).

On the family level, within Tenthredinoidea, the split of Argidae and Pergidae was estimated from the Early–Middle Jurassic (182–168 Ma) (Malagón-Aldana et al., 2021) to the earliest Early Cretaceous (143 Ma) (Wutke et al., 2024), with neither of the estimates contradicting the available age estimates for the superfamily. The crown-group Argidae, Pergidae and Tenthredinidae seem to have originated in the Early Cretaceous (124–100 Ma), contemporary with the Angiosperm Radiation and the Cretaceous Terrestrial Revolution (Peris & Condamine, 2024), Cimbicidae and possibly Diprionidae in the Late Cretaceous (90–76 Ma and 71–61 Ma, respectively) and Blasticotomidae in the latest Eocene (35–34 Ma) (Nyman et al., 2019; Wutke et al., 2024). In addition, Niu et al. (2022) recovered the Early Cretaceous (143–133 Ma) origin of the crown-group Athaliidae, which is considerably different from the mid-Eocene (41 Ma) estimate by Wutke et al. (2024), and only partially explainable by taxon sampling (see Wutke et al., 2024). Within Pamphilioidea, the age of crown-group Pamphiliidae was estimated to the mid-Eocene (41 Ma) and of Megalodontesidae to the early Miocene (18 Ma) (Wutke et al., 2024).

The oldest fossil associated with Tenthredinoidea is a blasticotomid †*Pseudoxylocerus bascharagensis* Nel et al. from the Early Jurassic Bascharage locality (~182 Ma) (used to calibrate stem Tenthredinoidea by Niu et al. (2022) and Wutke et al. (2024)), followed by several stem-group Blasticotomidae fossils from the Late Jurassic Karatau-Mikhailovka locality and Daohugou beds (~162 Ma). These and other younger Mesozoic fossils of Blasticotomidae were recognized as members of †Xyelotomidae, an extinct family that has been now synonymized with Blasticotomidae (Rasnitsyn & Müller, 2023). However, the sub-/family and even sometimes superfamily placement of these fossils is questionable (Nel et al., 2004). Thus, †*Palaeathalia laiyangensis* Zhang from the Early Cretaceous Tuanwang locality (~119 Ma) might be the oldest fossil more confidently placed within the crown-group Tenthredinoidea. The fossil was until recently considered the oldest Tenthredinidae, creating a long gap to the second oldest fossils, †*Tenthredo primordialis* Piton and †*Paleonematus jarzembowskii* Nel et al. from the Paleocene Menat locality (~60 Ma). However, Niu et al. (2022) suggested an alternative placement of †*P. laiyangensis* within the earlier branching family Athaliidae. The oldest Cimbicidae fossils, †*Cenocimbex menatensis* Nel and †*Hervetia paleocenica* Nel & Kundura, belong to an extinct subfamily and are also from the Paleocene Menat locality (~60 Ma). Fossil records of Argidae and Pergidae are relatively rare with the first representatives appearing in the Eocene (48–34 Ma), considerably later than the current estimates for the families.

In addition, the oldest fossil associated with Pamphilioidea is the poorly preserved †*Sogutia liassica* (†Xyelydidae) from the Early Jurassic Sogyuty locality (~196 Ma), followed by several better-preserved xyelydids from the Early Jurassic Sai-Sagul locality (~178 Ma). The oldest crown-group Pamphilioidea are probably several fossils from the Middle to Late Jurassic Daohugou beds (~162 Ma) placed in extant families Megalodontesidae and Pamphiliidae. Fossil Megalodontesidae are exclusively known from the Mesozoic and are all stem-group fossils. One of

the oldest Pamphiliidae fossils, †*Scabolyda orientalis* from the Daohugou beds (~162 Ma), has been recovered with very limited support within crown-group Pamphiliidae, but more confident placements of this and many other Pamphiliidae fossils await a more comprehensive phylogenetic analysis (Wang et al., 2016). The oldest fossils associated with Orussoidea are several †Paraorussidae fossils from the Middle Karatau-Mikhailovka locality (~162 Ma). The oldest Orussidae are †*Mesorussus taimyrensis* Rasnitsyn from the Late Cretaceous Taiymir amber (~97 Ma) and †*Minyorussus luzzii* Basibuyuk et al. from New Jersey amber (~92 Ma). These two species are probably stem Orussidae (Vilhelmsen, 2003; 2007), while the oldest crown-group Orussidae seems to be †*Baltorussus velteni* Schedl (Vilhelmsen & Zimmermann, 2014) and the recently described first female orussid fossils from Baltic amber, †*Kryptovelona carstengroehni* Vilhelmsen et al. and †*Orussus juttagroehnae* Vilhelmsen et al., from the Eocene (48–34 Ma) (Vilhelmsen et al., 2024). The oldest fossil placed in Siricoidea and Siricidae is †*Liasirex sogdianus* Rasnitsyn from the Sai-Sagul locality (~178 Ma), followed by several Siricidae and one †Protosiricidae fossils from Karatau-Mikhailovka locality (~162 Ma). However, some of these Cretaceous fossils originally associated with the crown-group Siricidae are deemed stem-group representatives, which makes two †*Urocerus ligniticus* (Piton) fossils from Paleocene of Menat (~60 Ma), the oldest clear crown-group Siricoidea (Jouault et al., 2020; Wedmann et al., 2014).

Overall, the crown-group age estimates are generally supported by the fossil record or at least do not contradict it. However, sometimes these age estimates are very close to the oldest crown-group fossils, as seen in the cases of Pamphilioidea and Siricoidea. At other times, they are considerably older than the most credible crown-group fossils, suggesting relatively long ghost lineages. For example, there is a 115–17 Ma gap between the first occurrence of †*Palaeathalia laiyangensis* and the age estimate for Tenthredinoidea. Similarly, there is a gap of around 40 Ma years between †*Tenthredo primordialis* Piton and the age estimate for Tenthredinidae, and more than 60 Ma between the first fossils of Argidae, Pergidae and the estimated crown-group ages for the families. To close these gaps, continued studies of the Symphyta fossil record are needed, together with revisions of the existing fossil record, as the placement of several early fossils, some used as calibration points in node dating studies, has been questionable. Some of the node dating studies made use of the total-evidence dating study of Ronquist et al. (2012) to help derive the calibration points, indicating a need for a comprehensive total-evidence dating study on Symphyta.

Proctotrupomorpha

Rasnitsyn (1988) erected the Infraorder Proctotrupomorpha, comprising the superfamilies Cynipoidea, Platygastridae, Chalcidoidea, Mymarommatoidea and Proctotrupoidea (including Diaprioidea). Sharkey (2007) later recognized Diaprioidea as a distinct superfamily, a finding in line with recent phylogenomic works. Proctotrupomorpha has been consistently recovered as monophyletic in other phylogenetic analyses using both morphology and multilocus data

(Downton et al., 1997; Heraty et al., 2011; Klopstein et al., 2013; Sharkey et al., 2012), and is also corroborated using phylogenomic data (Branstetter, Danforth, et al., 2017; Peters et al., 2017; Blaimer et al., 2023). However, the phylogeny within Proctotrupomorpha varied between the UCE-based studies (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017) and the transcriptomic analyses of Peters et al. (2017) (Figure 1, inset 2A/2B).

Blaimer et al. (2023) recovered a Late Triassic origin for Proctotrupomorpha (210 Ma), which is strikingly close to the age estimate of the preferred dating analysis of Peters et al. (2017) of 211 Ma (Figure 2). These estimates do not contradict the oldest known Proctotrupomorpha fossils from the Middle–Late Jurassic localities in China and Kazakhstan (~162 Ma) placed in the extinct (†)Peleserphidae and (†)Mesoserphidae and extant (Heloridae, Pelecinidae and Roproniidae) Proctotrupoidea families.

Proctotrupomorpha—Superfamily Cynipoidea

Within Proctotrupomorpha, gall wasps (Cynipidae) in the superfamily Cynipoidea were shown to be polyphyletic using transcriptome data (Peters et al., 2017), UCEs (Blaimer et al., 2020) and Benchmarking Universal Single-Copy Orthologs (BUSCOs) (Hearn et al., 2024), as multiple cynipid tribes were recovered outside of Cynipidae. This has major implications for the evolution of gall induction within Cynipoidea, where the long-held view of gall induction having evolved only once within a monophyletic Cynipidae from an entomophagous ancestor has now been refuted (Ronquist et al., 2015). According to our current understanding, the life history trait of gall induction has likely evolved at least six times independently, while inquilinism (living commensally within the gall) has evolved at least three times (Blaimer et al., 2020; Hearn et al., 2024). The wood-boring beetle parasitoids within the families Ibalidae and Liopteridae, which were previously considered to be the earliest divergent lineage within Cynipoidea (Ronquist et al., 2015), are now considered close relatives of Figitidae *sensu lato* (Blaimer et al., 2020). The newly established family Paraulacidae (formerly tribe Paraulacini) has been shown to be the sister group to the remaining Cynipoidea, all of which are parasitoids of gall-inducing Chalcidoidea (Hearn et al., 2024; Rasplus et al., 2022). Besides research on the higher level relationships of Cynipoidea, tailored studies on specific tribes and genera have also been conducted with phylogenomic data (e.g., Ward et al., 2022, 2024; Zhang, Buffington, et al., 2020). The recent phylogenomic studies on the former subfamilies of Figitidae, such as Parnipinae and Euceroptinae, suggest that they will likely have to be elevated to family level in the future (Blaimer et al., 2020, 2023). The Australian endemic Austrocynipidae, perhaps the rarest of all Hymenoptera families, has never been collected again since its initial discovery and has not been included in any phylogenomic analyses as of now.

Divergence time estimates for the crown-group Cynipoidea vary drastically between different studies, out of which only one (Blaimer et al., 2020) focused on Cynipoidea as a whole. The inferred ages span from the Early Jurassic (191 Ma) (Blaimer et al., 2020), to the Early

Cretaceous (130 Ma) (Blaimer et al., 2023) and Late Cretaceous (94 Ma) (Peters et al., 2017). Within Cynipoidea, the age of crown-group Ibalidae and Figitidae was estimated to the Early Cretaceous (113 and 123 Ma, respectively) (Blaimer et al., 2020; Buffington et al., 2012), of Cynipidae *sensu stricto* to the border between the Early and Late Cretaceous (103 Ma) (Blaimer et al., 2020), and of Liopteridae to the Late Cretaceous (77 Ma) (Blaimer et al., 2020).

The fossil record of Cynipoidea is relatively poor. The oldest fossils placed in Cynipoidea are from the Early Cretaceous, †*Dahurocynips dahurica* Rasnitsyn from the Turga Formation (~124 Ma) and †Archaeocynipidae from the Khasurty and Baissa localities and Gidarinskaya Formation (~119 Ma), although the placement of †Archaeocynipidae within Cynipoidea is questionable (Ronquist, 1999). Several fossils from the Late Cretaceous New Jersey (~92 Ma), Taimyr (105–83.5 Ma) and Canadian (~77 Ma) amber have been associated with crown-group Cynipoidea (Liu et al., 2007). The oldest known Figitidae are †*Protocharips evenhuisi* Kolarev, placed in the extant subfamily Charipinae from the Late Cretaceous Taimyr amber (~99 Ma), and two fossils from the New Jersey amber (~92 Ma) (Pujade-Villar & Peñalver, 2019; Table S3c). Only three fossil representatives of Liopteridae are known, all probably stem-group Liopteridae, with the two oldest ones from the Late Cretaceous Canadian amber (~77 Ma). The oldest known Cynipidae is †*Tanaoknemus ecarinatus* Liu et al., also from the Late Cretaceous Canadian amber (~77 Ma), but its position is uncertain. Thus, †*Kinseycynips succinea* (Kinsey) from Baltic amber (48–34 Ma) is considered the oldest crown-group Cynipidae (Liu et al., 2007). There are only three known fossils of Ibalidae, with two of the oldest specimens found in late Eocene Baltic amber (48–34 Ma), including one classified within the extant genus *Ibalia* (Liu et al., 2007).

The fossil record implies the existence of crown-group Cynipoidea in the early Late Cretaceous, suggesting that they must have originated at the latest during the Early Cretaceous and giving support to the age estimate from Blaimer et al. (2023). While the Early Jurassic estimate of Blaimer et al. (2020) might seem too old, we cannot exclude the Jurassic origin of the crown-group considering how poor the fossil record of Cynipoidea is. The lack of fossils might also justify the more than 70 Ma gap between the oldest known crown-group Ibalidae and Cynipidae and the age estimates for the families. Thus, moving forward, both better definition of Cynipoidea families and revision and improvement of the fossil record are needed to reconstruct the complex evolution of gall induction.

Proctotrupomorpha—Superfamily Platygastroidea

The superfamily Platygastroidea was traditionally recognized comprising two families, Platygastriidae and Scelionidae (Austin et al., 2005). Phylogenetic studies by Murphy et al. (2007) and Heraty et al. (2011) have independently found that Scelionidae was paraphyletic. The family was merged with Platygastriidae by Sharkey (2007) without additional analysis. The superfamily was recently extensively revised using multilocus data in combination with morphological and transcriptomic

data, now formally recognizing seven extant families (Chen et al., 2021). This treatment also restores Scelionidae as a monophyletic family after Neuroscelionidae and Sparasionidae have been split off, rather than as a subfamily of Platygastriidae *sensu* Sharkey (2007). Three additional small families including Nixoniididae (16 species), Geoscelionidae (three extant species) and the monotypic Janzenellidae were formally erected as new families. The plesiomorphic hosts of the superfamily are likely Orthoptera eggs, while the group may have subsequently shifted onto eight other insect orders, including major radiations of lineages attacking Lepidoptera, Araneae and Diptera (Chen et al., 2021).

The age of the superfamily is estimated to the Early Cretaceous (146–126 Ma) (Blaimer et al., 2023; Peters et al., 2017; Tang et al., 2019) (Table S2), while the age estimates for constituent families and a comprehensive dated phylogeny of the platygastroids are still missing. Talamas et al. (2017) report the oldest clear platygastroids from the Early Cretaceous Lebanese amber (~128 Ma), while the oldest described fossil is a †*Proterosceliopsis*, †*Proterosceliopsis masneri* Ortega-Blanco et al. from the Early Cretaceous Álava amber (~102 Ma). These are followed by several fossils in the Late Cretaceous Burmese amber and Bezonais amber (~97 Ma) placed in †*Cardiophyodidae*, and extant families Geoscelionidae, Platygastriidae and Sparasionidae (Talamas et al., 2017, 2019; Table S3c). However, the placement of many platygastroid fossils is questionable given that the relationships within the superfamily and monophyly of some families are still being scrutinized. Nevertheless, there have recently been some positive examples of using novel microscopy techniques and microcomputed tomography (micro-CT) scanning for examining morphology to classify both extant and fossil families of platygastroids (Bremer et al., 2021; Mikó et al., 2021). For example, Mikó et al. (2021) recently reported new family-level morphological characters for Platygastriidae, which support sister relationships of the recently erected family Janzenellidae and Platygastriidae, and provide additional evidence for the classification of fossils.

Proctotrupomorpha—Superfamilies Chalcidoidea and Mymarommatoidea

Perhaps the greatest number of recent higher level taxonomic changes within Hymenoptera pertains to the megadiverse superfamily Chalcidoidea. Extensive taxonomic reorganization occurred as a result of the combined effort of AHE and UCE studies (Cruaud et al., 2024; Zhang, Heraty, et al., 2022). The Zhang, Heraty, et al.'s (2022) study revised the planidial clade, erecting Eutrichosomatidae and Chrysolampidae as new families. Burks et al. (2022) split the polyphyletic family Pteromalidae into 24 families, and Eupelmidae into three families to reflect the results of the Cruaud et al. (2024) phylogeny, bringing the total number of extant chalcidoid families to 50 (Burks et al., 2022; Zhang, Heraty, et al., 2022). While the higher classification of Chalcidoidea is likely far from stable, phylogenomic studies on various families with improved sampling will undoubtedly improve our understanding (Baker et al., 2020; Cruaud et al., 2021; Maletti

et al., 2021; Peters et al., 2018; Rasplus et al., 2020; van Noort et al., 2024; Zhang, Heraty, et al., 2022; Zhang, Sheikh, et al., 2022). The earliest lineages within this megadiverse superfamily, along with its sister group Mymarommatoidea, are egg parasitoids (Cruaud et al., 2024; Peters et al., 2018). Subsequently, the shift from smaller soft-bodied wasps to larger and more heavily sclerotized wasps coincides with radiations of host insect diversification, and they are currently found in virtually all orders and life stages of Holometabola (Cruaud et al., 2024). Phytophagy has also evolved many times across Chalcidoidea, with the first shifts coinciding with the early diversification of terrestrial angiosperms ~100 Ma (Cruaud et al., 2024).

Comprehensively sampled divergence dating analyses suggest a Middle Jurassic (169–162 Ma) (Blaimer et al., 2023; Cruaud et al., 2024) to the Early Cretaceous (143–127 Ma) (Peters et al., 2017, 2018; Tang et al., 2019; Zhu et al., 2023) origin of crown-group Chalcidoidea, with a rapid diversification during the Early to Late Cretaceous in southern Gondwana, including subsequent dispersals to the northern Hemisphere. Zhang, Heraty, et al. (2022) dated the origin of a planidial larva clade to the Early Cretaceous (111 Ma) and the evolution of ant parasitism within the clade to the Paleocene (64 Ma). The most comprehensive age estimates for different chalcidoid families can be found in Cruaud et al. (2024). Blaimer et al. (2023) included a single representative of the superfamily Mymarommatoidea and estimated its divergence from Chalcidoidea to the Early Jurassic (180 Ma). A comparable age for this divergence (174 Ma) was recovered by Cruaud et al. (2024) (Table S2).

The Chalcidoidea are present in the fossil record since the Early Cretaceous, with the oldest being several fossils from Lebanese amber (~128 Ma) belonging to the genera †*Cretaxenomerus* and †*Protoita* (†*Protoitidae*). Ulmer et al. (2023) suggested a stem position for †*Protoitidae*. The second oldest fossil is a †*Baeomorpha* (*Baeomorpha*idae) from the Early–Late Cretaceous El Soplao amber (~110 Ma), followed by †*Baeomorpha liorum* Huber et al. and †*Myanmymar aresconoides* Poinar & Huber (*Mymaridae*) from the Late Cretaceous Burmese amber (~97 Ma) and several †*Baeomorpha* fossils from Taimyr amber (~99–85 Ma). No other extant chalcid family is known from the Cretaceous (excluding some doubtful placements or undescribed specimens of eupelmids and pteromalids from Jordanian amber). Furthermore, only a few extant families are documented from the early Eocene (*Encyrtidae*, *Eulophidae*, *Eurytomidae*, *Pirenidae*), while several others appear for the first time during the late Eocene in Baltic amber (48–34 Ma). The oldest fossil associated with Mymarommatoidea is †*Cretaceomma libanensis* Rasnitsyn et al. from the Early Cretaceous Lebanese amber (~128 Ma), followed by †*Archaeomma hispanicum* Ortega-Blanco et al. from El Soplao amber (~110 Ma) (Table S3c).

The current Middle Jurassic age estimate (Cruaud et al., 2024) for the crown-group Chalcidoidea creates a 30 Ma gap to the oldest clear crown-group representative of *Baeomorpha*idae. In addition, the Early Cretaceous diversification is poorly supported by the fossil record, as it assumes that the crown-group representatives of most of the families should be present at least during the Late Cretaceous. Nevertheless, the estimated timing of diversification of chalcid lineages

corresponds to major events in the evolution of angiosperms as well as host insects (Cruaud et al., 2024), while the fossil record of chalcids is severely understudied. Moreover, most of the chalcids are, due to their small size, known only from amber deposits, which propagates the temporal and spatial gaps in the already patchy fossil record of Hymenoptera. The gaps between the age estimates and fossil record will hopefully narrow down in the future with the upcoming revision of the chalcid fossil record (J.-Y. Rasplus, pers. comm.), increased interest in the fossil record of this group and the application of the novel imaging techniques and micro-CT scanning necessary to study these Microhymenoptera.

Proctotrupomorpha—Superfamilies Diaprioidea and Proctotrupeoidea

The superfamilies Diaprioidea and Proctotrupeoidea within Proctotrupomorpha have yet to receive comprehensive phylogenomic treatment. While both groups were included in the study by Blaimer et al. (2023) and Diaprioidea was included in Cruaud et al. (2024), the taxonomic sampling was comparatively limited. Within Diaprioidea, Diapriidae was recovered as polyphyletic, with Belytinae and Ambositrinae forming a monophyletic group, while Ismaridae is embedded within Diapriidae (Blaimer et al., 2023; Cruaud et al., 2024). As for Proctotrupeoidea, Roproniidae was not recovered within the superfamily in the two UCE studies using two separate samples of *Ropronia garmani* Ashmead, but as the sister group to Chalcidoidea + Diaprioidea, and this clade, in turn, formed the sister group to Proctotrupeoidea (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017) (Figure 1, inset 2A/2B). This result was not supported by some morphological and all multilocus studies that have included this taxon (Heraty et al., 2011; Klopstein et al., 2013; Sharkey et al., 2012). Three rare families of Proctotrupeoidea, the two Australian endemic families Austroniidae and Peradeniidae, along with the eastern Palearctic endemic family Proctorenyxidae have not been included in any phylogenomic analyses to date.

The divergence date estimates suggest a Jurassic origin of crown-group Proctotrupeoidea (175–161 Ma) (Blaimer et al., 2023; Peters et al., 2017; Tang et al., 2019) and a Late Jurassic–Early Cretaceous origin of Diaprioidea (~145 Ma) (Blaimer et al., 2023; Tang et al., 2019). In addition, Blaimer et al. (2023) estimated the age of Diapriidae *sensu lato* to the Early Cretaceous (114 Ma) and Proctotrupidae to the Late Paleocene (57 Ma) (Table S2).

There are more than 50 fossils from various Late Jurassic localities (~160 Ma) associated with Proctotrupeoidea, belonging to different fossil and extant (Heloridae, Peleciniidae and Roproniidae) families. Members of Proctotrupidae are present in the fossil record since the earliest Early Cretaceous (~143 Ma), while the oldest fossil placed in crown-group Proctotrupidae is †*Cresogmus grimaldii* Rasnitsyn et al. from Burmese amber (~97 Ma), the only known Proctotrupidae from the Late Cretaceous. The later occurrences include several fossils identified as Proctotrupidae from the early Eocene. The oldest fossil placed in Diaprioidea is †*Mymaropsis baabdaensis* Krogman et al.

from Early Cretaceous Lebanese amber (~128 Ma), placed in †Spathiopterygidae, followed by †*Cretapria tsukadai* Fujiyama from Early Cretaceous Choshi amber (~117 Ma), currently placed in Ismaridae but potentially also belonging to †Spathiopterygidae (Rasnitsyn & Öhm-Kühnle, 2020; Table S3c). Thus, the oldest described crown-group Diaprioidea might be a betyline †*Protobelyta monsirei* Jouault et al. from Early Cretaceous Hkamti amber (~111 Ma) and the oldest crown-group Diapriidae †*Gaugainia electrogallica* Perrichot & Nel from Charentese amber (~102 Ma).

The younger age estimates for crown-group Proctotrupeoidea seem too close to the oldest crown-group fossils, especially the estimate from Peters et al. (2017), who included only two proctotrupoids, and Tang et al. (2019), who although had denser sampling of the superfamily, applied relatively narrow uniform calibration points with soft maximum. In addition, the age estimates for crown-group Proctotrupidae are clearly too young given the fossil record. The current Jurassic age estimates for the crown-group Diaprioidea are in line with the fossil record, while the estimates for the crown-group Diapriidae *sensu lato* are also relatively close to the oldest crown-group representatives.

Evaniomorpha *sensu lato*

The monophyly of the smaller parasitoid superfamilies formerly known as Evaniomorpha (Evanoidea, Trigonoidea, Ceraphronoidea, Stephanoidea and Megalyroidea) *sensu* Rasnitsyn (1988) has always been controversial, and these groups have received comparatively little taxonomic attention to this date. Using multilocus data, they have been recovered either as a monophyletic group (Downton et al., 1997; Klopstein et al., 2013) or a paraphyletic grade in relation to Aculeata (Heraty et al., 2011; Sharkey et al., 2012). While the traditional Evaniomorpha *sensu* Rasnitsyn (1988) remains poorly represented in large phylogenomic studies, the monophyly of this group is not supported in all recent studies and their relationships remain controversial, especially with respect to the phylogenetic position of Ceraphronoidea (Figure 1, inset 4A/4B). However, it is worth noting that all studies that have included either Trigonoidea and/or Megalyroidea, have recovered the two as sister to the Aculeata (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Heraty et al., 2011; Klopstein et al., 2013; Peters et al., 2017). The divergence date estimate for Evaniomorpha + Aculeata is Late Triassic (225–206.2 Ma) (Blaimer et al., 2023; Peters et al., 2017).

Evaniomorpha—Superfamilies Trigonoidea and Megalyroidea

Trigonoidea (consisting of a single family Trigonalidae) has been either recovered as the sister group to Aculeata in Peters et al. (2017) and Branstetter, Danforth, et al. (2017), or as sister to Megalyroidea (consisting of a single family Megalyridae), which then together formed the sister group to Aculeata (Blaimer et al., 2023;

Heraty et al., 2011; Klopstein et al., 2013). Most of the dating studies focusing on Hymenoptera included only a single to a couple of representatives of the two superfamilies, thus only ages of stem-groups are provided. Tang et al. (2019) estimated the age of the crown-group Megalyroidea to the Middle Jurassic (160 Ma) and of Trigonaloidea in the Early Cretaceous (125 Ma).

As the position of †Maimetschidae within Trigonaloidea is unclear, only fossils placed in Trigonalidae are considered. Nel et al. (2003) reviewed the Trigonalidae fossil record and concluded that almost all fossils previously associated with Trigonalidae should be considered *incertae sedis* and that the oldest certain fossil is †*Albiogonaly elongatus* Nel et al., although Boudinot et al. (2022) tentatively retained the fossil as *incertae sedis* in Trigonaloidea. The oldest Megalyroidea fossils are from the Late Jurassic Karatau-Mikhailovka and Yujiagou localities (~162 Ma) (Table S3c). Some of the fossils from the early Late Cretaceous amber deposits, e.g., species of †*Kamyristi* and †*Cretodinapsis* (~97 Ma), were recently recovered with limited support within the crown-group Megalyridae (Brazidec et al., 2024), suggesting that crown-group Megalyroidea may have originated already during the Early Cretaceous. However, the better supported crown-group representative of Megalyroidea is †*Prodinapsis oesienensis* Perrichot from the early Eocene Oise amber (~52 Ma).

Evaniomorpha—Superfamilies Evanioidea and Stephanoidea

Evanioidea and Stephanoidea have consistently been recovered as sister groups (Blaimer et al., 2023; Peters et al., 2017). Within Evanioidea, Evaniidae and Gasteruptiidae have been investigated more extensively using multilocus data by Sharanowski et al. (2019) and Parslow et al. (2020), respectively.

Based on node dating studies, crown-group Evanioidea originated sometime between the Early and Late Jurassic (178–151 Ma) (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Parslow et al., 2020; Peters et al., 2017). A tip dating study (Jouault et al., 2022) similarly recovers an Early Jurassic origin for the crown-group (176 Ma). The age estimate for the crown-group Evaniidae ranges from the Early Cretaceous (137 Ma) (Sharanowski et al., 2019) to Paleocene (58 Ma) (Jouault et al., 2022), and for Gasteruptiidae vary from Paleocene (60 Ma) (Parslow et al., 2020) to the latest Oligocene (23 Ma) (Jouault et al., 2022). Peters et al. (2017) recovered a Late Triassic origin of the crown-group Stephanoidea (214 Ma). In a recent tip dating study based on morphological data, Ge et al. (2023) estimated a Late Jurassic (155 Ma) origin of crown-group Stephanidae.

There has been a recent phylogenetic revision of the fossil record of the superfamily Evanioidea (Jouault et al., 2022), making differentiation of crown- and stem-group fossils relatively straightforward. The oldest stem-group fossils associated with the superfamily belong to †Anomopterellidae and †Praeaulacidae from Middle–Late Jurassic localities (~162 Ma). The oldest fossil recovered within crown-group Evanioidea is †*Cretevania concordia* Rasnitsyn et al. from the Early Cretaceous Old Pit, Clockhouse Brickworks (~133 Ma), which is also

one of the oldest stem Evaniidae. The earliest crown-group Evaniidae fossils are known from the Eocene Baltic amber (48–34 Ma). There are only three fossils associated with Gasteruptiidae, all likely stem-group fossils, the oldest being †*Kotujisca kholbotensis* Rasnitsyn from the Early Cretaceous Kholbotu-Gol locality (~129 Ma). The oldest stem-group Aulacidae are described from the Late Cretaceous Burmese amber (~97 Ma), while the oldest crown-group Aulacidae is †*Pristaulacus jarzembowskii* Jouault & Nel from the Paleocene Menat locality (~60 Ma). The oldest fossil currently belonging to Stephanoidea is †*Cretephialites pedrerae* Rasnitsyn & Ansoerge from the La Pedrera de Rúbies Formation (~128 Ma), which was transferred to †Ohlhoffiidae by Jouault et al. (2021). The oldest crown-group Stephanoidea are probably several fossils from Burmese amber (~97 Ma) recovered within crown-group Stephanidae in the Ge et al. (2023) analysis (Table S3c).

According to Li et al. (2018), the Early Jurassic origin of stem Evanioidea, together with the Middle to Late Jurassic diversification of its lineages, appears to conform best to the fossil record, which is generally in agreement with the available age estimates. This agreement between the age estimates and fossil record could be attributed to the well-defined stem- and crown-group lineages of Evanioidea as a result of the recent revision of the fossil record (Jouault et al., 2021). Furthermore, the Late Jurassic estimate for the origin of crown-group Stephanidae is ~60 Ma older than the oldest likely crown-group representatives, but this age is not unlikely given the overall fossil record of the group (Li et al., 2017).

Evaniomorpha—Superfamily Ceraphronoidea

The positioning of Ceraphronoidea remains uncertain (Figure 1, inset 4A/B), as it has been recovered as the sister group to Ichneumonoidea (Peters et al., 2017; Blaimer et al., 2023), sister to Evanioidea + Trigonaloidea/Aculeata (Branstetter, Danforth, et al., 2017), or sister to Evanioidea + Stephanoidea (Blaimer et al., 2023). To date, no comprehensive phylogeny exists for either Megaspilidae or Ceraphronidae, as this superfamily is one of the least studied lineages of Hymenoptera. However, both families appear to be monophyletic in the limited number of published phylogenetic/-omic studies (Blaimer et al., 2023; Dowton et al., 1997; Heraty et al., 2011; Klopstein et al., 2013; Peters et al., 2017).

There are no dating studies focusing on Ceraphronoidea available to date. Peters et al. (2017) and Blaimer et al. (2023) recovered similar age estimates for the superfamily in the Early Jurassic (136–121 Ma) (Table S2). The oldest fossil associated with Ceraphronoidea (excluding the extinct families with uncertain placement in Ceraphronoidea; Table S1b) is †*Conostigmus dolicharthrus* Alekseev & Rasnitsyn (Megaspilidae) from Taimyr amber (~99 Ma), followed by †*Prolagynodes penniger* Alekseev & Rasnitsyn from a younger locality of Taimyr amber (~85 Ma) and †*Conostigmus cavannus* McKellar et al. from Canadian amber (~77 Ma) (Table S3c). Thus, the Early Jurassic age estimates for crown-group Ceraphronoidea seem reasonable given the current state of knowledge of the fossil record.

Superfamily Ichneumonoidea

The large superfamily Ichneumonoidea, which includes the two extant families Ichneumonidae and Braconidae, has been recovered as the sister group to the rest of Apocrita in studies using UCEs (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017), or as the sister group to Ceraphronoidea using both transcriptome and UCE data (Blaimer et al., 2023; Peters et al., 2017; Figure 1, inset 3). Chen and van Achterberg (2019) recently summarized 30 years of research for the systematics and phylogenetics of braconid wasps. The subfamilies Apozyginae, Trachypetinae and Masoninae had uncertain placements within the superfamily (e.g., see Quicke et al. (2020)), but have since been grouped within Braconidae in light of a recent UCE phylogeny and re-interpreted morphological evidence (Jasso-Martínez et al., 2022). Within subfamilies of Braconidae, only a select few subfamilies such as Rogadinae have received thorough examination using phylogenomic data (Jasso-Martínez et al., 2021; Samacá-Sáenz et al., 2021). Ichneumonidae, the species-richest family of Hymenoptera, has been recovered consistently as monophyletic using different targeted capture methods. These studies have also established Xoridinae as the sister group to the remaining ichneumonids, and identified a rapid radiation in the early evolution of Ichneumonidae (Klopfstein et al., 2019; Sharanowski et al., 2021). Relationships within two of three major informal groupings, Ichneumoniformes and Pimpliformes, have also been interrogated using phylogenomic data (Klopfstein et al., 2019; Santos et al., 2019, 2021, 2022). Nevertheless, Ophioniformes and the backbone of the ichneumonid tree remain poorly resolved, especially regarding the position of the enigmatic Labeniformes and various small subfamilies. Thus, the exact relationships within the family are still in need of extensive study (Blaimer et al., 2023; Sharanowski et al., 2021).

Both Peters et al. (2017) and Blaimer et al. (2023) report an Early Jurassic origin for crown-group Ichneumonoidea (182 and 207 Ma, respectively). The age estimates for the two constituent extant families vary considerably between different studies, and comprehensive age estimates are lacking. Whitfield (2002) provided the first age estimates for Braconidae and microgastroids using a penalized likelihood approach, followed by Murphy et al. (2008) who also applied penalized likelihood but newly derived calibration points. In a node dating study, Peters et al. (2017) recovered an Early Cretaceous origin of the crown-group Braconidae (145 Ma) and Ichneumonidae (106 Ma). However, Blaimer et al. (2023) recovered much older estimates for both families, with the crown-group Braconidae originating in the Early Jurassic (185 Ma) and Ichneumonidae at the Late Jurassic–Early Cretaceous boundary (142 Ma). A recent total-evidence dating study focused on the ichneumonid grouping Pimpliformes, recovered an even older, Early Jurassic origin for the crown-group Ichneumonidae (181 Ma) (Spasojevic et al., 2021), suggesting that most of the extant ichneumonid subfamilies originated before the Cretaceous–Paleogene boundary.

A few select studies focus on lower taxonomic levels of Braconidae, such as the node-dating studies on Rogadinae and Doryctinae (Zaldivar-Riverón et al., 2008; Zaldivar-Riverón et al., 2008). Kittel et al. (2016) used the braconid subfamily Cheloninae to demonstrate

an enormous impact of dating method choice, calibration points and calibration priors on the age estimates, reporting median age estimates from the Eocene (45 Ma, penalized likelihood) to the Late Triassic (205 Ma, total-evidence tip dating) for the subfamily. Within Ichneumonidae, Santos et al. (2022) recently conducted a total-evidence dating study on Labeninae (Santos et al., 2022), addressing the role of Gondwanan vicariance in the diversification of this subfamily.

The oldest fossil placed in Ichneumonoidea is a braconid †*Cretobraconus maculatus* Rasnitsyn & Sharkey from the Late Jurassic Khutuliyn-Khira locality (~149 Ma) currently with uncertain but likely stem position within braconids. The oldest braconid fossil associated with an extant subfamily (Aphidiinae) is †*Archephedrus stolamissus* Ortega-Blanco et al. from the Álava amber (~102 Ma). The oldest certain Ichneumonidae are members of †Paleoichneumoninae, the oldest occurrence being †*Palaeoichneumon townesi* Kopylov from the Early Cretaceous Kholbotu-Gol locality (~129 Ma). Their position within Ichneumonidae (stem vs. crown), as well as the position of two subsequent subfamilies in the fossil record, †Novichneumoninae (~99 Ma) and †Labenopimplinae (~99–77 Ma), is still debatable. †Labenopimplinae were, however, clearly recovered within crown-group ichneumonids in the total-evidence dating study of Spasojevic et al. (2021). The oldest fossils currently placed in an extant subfamily are †*Albertocryptus dossenus* McKellar et al. (Labeninae) from the Late Cretaceous Canadian amber (~77 Ma) and †*Hallocinetus arvensis* (Piton) (Acaenitinae) from Paleocene of Menat (~60 Ma). However, their current placement is highly uncertain (McKellar et al., 2013; Santos et al., 2022; Spasojevic et al., 2022), making fossils from the Fur Formation (~51 Ma) the earliest clear crown-group representatives of extant ichneumonid subfamilies (Klopfstein, 2022; Viertler et al., 2022; Table S3c).

The fossil record suggests the presence of the crown-group Braconidae and likely Ichneumonidae during the entire Late Cretaceous, making the estimate of Peters et al. (2017) for the crown-group ichneumonids too young. With a comprehensive total-evidence-dated UCE phylogeny of ichneumonids (B. Santos and A. Viertler pers. comm.) and a node-dated UCE phylogeny of braconids (J. Jasso-Martínez pers. comm.) on the way, we are soon to see more credible age estimates for both families. The fossil record of braconids has received particularly limited attention, and the careful assessment of the calibration points will be crucial for improving the current age estimates.

Aculeata

Different age estimates suggest that crown-group Aculeata originated between the Early Jurassic and the earliest Early Cretaceous (~195–142 Ma) (Blaimer et al., 2023; Boudinot et al., 2022; Branstetter, Danforth, et al., 2017; Tang et al., 2019). However, the two analyses specifically focusing on Aculeata (Boudinot et al., 2022; Branstetter, Danforth, et al., 2017) both inferred a Middle Jurassic origin for the group (~175–161 Ma). Wilson et al. (2013) also provided age estimates for the constituent superfamilies and families, associating their diversification with the diversification of flowering plants during Cretaceous.

According to Boudinot et al. (2022), the oldest definitive crown-group Aculeata are from Early Cretaceous Lebanese amber (~128 Ma), belonging to the traditional Chrysoidea and †Holopselellidae, which they recovered close to Bethyloidea and †Chrysothyridae. These fossils suggest that the Early Cretaceous age estimates for crown-group Aculeata are plausible, but possibly too young.

Aculeata—Superfamilies Chrysoidea and Dryinoidea

Among the aculeates, the phylogeny of the superfamily Chrysoidea stands out as a continuing and unresolved challenge. Klopstein et al. (2013) included four families of Chrysoidea (Bethyloidea, Chrysoidea, Plumariidae and Scoliidae) using seven genes, and recovered a paraphyletic grade to the rest of the aculeates with Bethyloidea as the sister to Vespoidea, rather than a monophyletic superfamily. Using transcriptome data, Peters et al. (2017) recovered a monophyletic superfamily Chrysoidea, whereas other studies consistently found it as paraphyletic with respect to the remaining Aculeata (as shown in Figure 1). However, the sampling of the respective studies can explain some of the inconsistencies: Peters et al. (2017) included representatives from three out of the seven families (Chrysoidea, Bethyloidea, Plumariidae), while Pauli et al. (2021) also included Dryinoidea. UCE studies (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017) additionally included Sclerogibbidae, Embolemidae and finally all seven extant families with the addition of Scoliidae (Boudinot et al., 2022). In the UCE studies, three families (Sclerogibbidae, Embolemidae and Dryinoidea) formed a separate clade, which was recovered as the sister group to the remaining Aculeata. This clade, which is referred to as 'Chrysoidea 2' in Branstetter, Danforth, et al. (2017), is not sampled in Peters et al. (2017), hence explaining the unlikely monophyly of the superfamily. Some recent studies have classified this group as the superfamily Dryinoidea to resolve the paraphyly of Chrysoidea in the old sense (Boudinot et al., 2022; Lepeco & Melo, 2023). Since there is little compelling evidence that Chrysoidea in the old sense is a monophylum, we here also recognize Dryinoidea as a separate superfamily (Figure 1). Despite the differences in taxon sampling, additional incongruences center around the position of Bethyloidea with respect to Chrysoidea and Scoliidae. Multiple studies have found Plumariidae as the sister group to Bethyloidea (Branstetter, Danforth, et al., 2017; Pauli et al., 2021; Peters et al., 2017), whereas Blaimer et al. (2023) and Boudinot et al. (2022) found Plumariidae as sister to the remaining lineages of this clade. On the family level, only Chrysoidea have been examined using multilocus and phylogenomic data, and while the family is monophyletic, some of the lower level classifications remain artificial (Pauli et al., 2019, 2021).

In dating studies in which the superfamily has been recovered as monophyletic, the age estimates range from the Early Jurassic to the Early Cretaceous (176–135 Ma) (Peters et al., 2017; Wilson et al., 2013). Several studies estimated the Early Cretaceous as the period of initial chrysooid diversification (Blaimer et al., 2023; Lucena & Almeida, 2022; Peters et al., 2017). In addition, Blaimer et al. (2023) reported an Early–Late Cretaceous (99 Ma) origin for crown-group

Chrysoidea, while the tip dating study by Lucena and Almeida (2022) reported a slightly older Early Cretaceous (~125 Ma) estimate for the family (Table S2). The age of crown-group Bethyloidea was estimated to the Early–Late Cretaceous (102 Ma) (Blaimer et al., 2023).

The oldest fossils associated with Chrysoidea are several fossils belonging to Bethyloidea and Scoliidae from the Early Cretaceous Lebanese amber (~128 Ma). The oldest fossil currently placed in Chrysoidea is †*Dahurochrysis veta* Rasnitsyn from the Turga locality (~124 Ma), but Melo and Lucena (2019) suggest that it might be a stem Chrysoidea. This fossil is followed by several fossils in the Late Cretaceous Burmese and Charentese amber (~97 Ma), some of which are recovered within crown-group Chrysoidea, but sometimes lack some of the morphological synapomorphies of the related extant taxa (Boudinot et al., 2022; Lucena & Melo, 2018). The oldest Dryinoidea are three fossils from Lebanese and Wealden amber (~128 Ma), each belonging to one of the three extant families (Table S3c).

If the chrysooids from the Burmese amber indeed belong to the crown-group, the age estimates from Blaimer et al. (2023) are too young and the crown-group must have originated at least during the Early Cretaceous. However, little can be concluded at this point, given the unstable relationships within Chrysoidea and even within Chrysoidea, as well as the uncertain placement of the Cretaceous fossils.

Aculeata—Superfamily Scoliidae

The paraphyly of the traditional Vespoidea resulted in the split into six superfamilies, largely based on the multilocus phylogeny present by Pilgrim et al. (2008). Scoliidae includes Scoliidae and Bradynobaenidae (Pilgrim et al., 2008), with an extensive phylogenomic analysis of Scoliidae available as a preprint (Khouri et al., 2022). The origin of crown-group Scoliidae was estimated to the Early Cretaceous (130–104 Ma) (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Wilson et al., 2013). The origin of crown-group Scoliidae was estimated to the Early Cretaceous (120–118 Ma), with some estimates being in conflict with the available age estimates for the superfamily (Khouri et al., 2022; Wilson et al., 2013). The origin of crown-group Bradynobaenidae was estimated to the Late Cretaceous (85 Ma) (Wilson et al., 2013).

There are several fossils from the Early Cretaceous localities of Spain and China (~128–119 Ma) that are currently considered putative Scoliidae (Boudinot et al., 2022; Haichun et al., 2002; Tables S2 and S3c), which suggest that most of the age estimates for the crown-group Scoliidae and Scoliidae are too young. Moreover, only the confidence intervals for the age estimates from Khouri et al. (2022) would encompass the age of these fossils (Haichun et al., 2002; Tables S2 and S3c).

Aculeata—Superfamilies Pompiloidea, Tiphiidae, Thynnoidea and Sierolomorphae

We follow the superfamily classification that was outlined by Pilgrim et al. (2008) and expanded with the recognition of Sierolomorphae

as a superfamily (Branstetter, Danforth, et al., 2017). According to this classification, the superfamily Pompiloidea comprises the families Pompilidae, Sapygidae, Mutillidae, as well as the newly elevated former mutillid subfamily Myrmosidae, as corroborated by genomic data (Johnson et al., 2013; Waldren et al., 2023). This classification is in slight contrast to the classification outlined in the preprint publication of Boudinot et al. (2022), who argue for a Pompiloidea in a wider sense, with the inclusion of several superfamilies elevated by Pilgrim et al. (2008) as families and not as separate superfamilies. To this end, they consider the superfamily Pompiloidea to include Sierolomorphidae, Tiphidae, Chyphotidae, Thynnidae, Pompilidae, Mutillidae and Sapygidae, thus reducing the number of superfamilies for this clade from four to one. Notably, the phylogenetic findings are not necessarily in disagreement and both classifications yield natural groupings. Until Boudinot et al. (2022) is formally published in peer-reviewed form, we here follow Pilgrim et al. (2008) as displayed in Figure 1. On the family-level, only Mutillidae have been investigated with deep taxonomic sampling and phylogenomic level data, and have been found to be monophyletic (Waldren et al., 2023).

The origin of crown-group Pompiloidea was estimated to the Early–Late Cretaceous (~100 Ma) by Wilson et al. (2013), Branstetter, Danforth, et al. (2017) and Blaimer et al. (2023), while Peters et al. (2017) and Waldren et al. (2023) recovered slightly older estimates, from the Late Jurassic to the Early Cretaceous (154–143 Ma). On the family level, based on a comprehensive molecular phylogeny of Pompilidae and four calibration points, Waichert et al. (2015) inferred a mid-Eocene (43 Ma) origin for the crown-group Pompilidae and a late Eocene diversification for the most diverse subfamilies, followed by an Oligocene diversification for the remaining subfamilies. More recently, Waldren et al. (2023) dated the origin of Mutillidae and Sapygidae to the Early Cretaceous (122 and 113 Ma, respectively), the origin of Pompilidae to the Late Cretaceous (71 Ma), and that of Myrmosidae to the Paleocene (65 Ma) (Table S2). Some studies using node dating techniques focused on lower taxonomic levels of Pompilidae. To this end, Rodriguez et al. (2015) estimated the origin of the pompilid tribe Aporini to the Miocene.

According to Waldren et al. (2023), the youngest Early Cretaceous age estimates for the crown-group Pompiloidea are not in alignment with what they deem the oldest pompiloid fossil, the sapygid wasp †*Cretofedschenkia santanensis* Osten (~117 Ma). Furthermore, most of the age estimates for the families in Waldren et al. (2023) are older than in the previous studies, but they are also in better agreement with the oldest known fossil of Sapygidae and of Pompilidae, †*Cryptocheilus leleji* Waichert, Rapoza & Rodriguez from the Eocene Fur Formation (~52), as elaborated in Waldren et al. (2023).

Thynnoidea includes Chyphotidae and Thynnidae, while Tiphioidea used to include Tiphidae and Sierolomorphidae (Pilgrim et al., 2008). However, Sierolomorphidae was not recovered as the sister group to Tiphidae using UCE data and thus was considered a separate superfamily Sierolomorphoidea (Branstetter, Danforth, et al., 2017). The current estimates suggest that the crown-group Thynnoidea and Tiphioidea originated during the Early Cretaceous (120–100 and 140–100 Ma, respectively) (Peters et al., 2017;

Wilson et al., 2013) or Late Cretaceous (~80 and ~70 Ma, respectively) (Blaimer et al., 2023).

The oldest fossil associated with Thynnoidea is †*Architiphia rasnitsyni* Darling & Sharkey from the Crato locality (~117 Ma), although this placement is not recovered by Boudinot et al. (2022). The second oldest fossil is †*Myzine madeleineae* Piton from Menat (~60 Ma), followed by several fossils from the Florissant Formation (~36 Ma). The oldest fossils associated with Tiphioidea are †*Thanatotiphia nyx* Engel et al. and †*Burmatiphia mandibulata* Zheng et al. from Burmese amber (~97 Ma). The latter was suggested to be a stem lineage of Tiphidae, while the placement of the former is unclear, but possibly nested within the crown-group Tiphidae, which would imply that some of the available age estimates for the superfamily are too young. In contrast, the oldest clear fossils of Thynnoidea are significantly younger than the current age estimate for the superfamily. The only fossil currently placed in Sierolomorphidae is †*Loreisomorpha nascimbenei* Rasnitsyn from New Jersey amber (~92 Ma) (Table S3c).

Aculeata—Superfamily Vespoidea

Vespoidea was refined to only include the two families Rhopalosomatidae and Vespidae (e.g., Branstetter, Danforth, et al., 2017; Wilson et al., 2013). Recent work with extensive sampling recovered the two clades that include the eusocial lineages, Stenogastrinae and Polistinae + Vespinae, as rather distantly related, thus once more strongly suggesting two separate origins of eusociality within the family using different targeted capture data (Bank et al., 2017; Piekarski et al., 2018). This finding was originally revealed about 10 years prior in a well-supported multi-locus phylogeny, albeit with much smaller taxon sampling (Hines et al., 2007). Despite the new, recent work on the phylogeny of Vespidae, the phylogenetic placement of the family Vespoidea in relationship with other Aculeates is highly unstable: Branstetter, Danforth, et al. (2017) recovered it as sister to the clade containing Sierolomorphoidea, Pompiloidea, Tiphioidea and Thynnoidea; Blaimer et al. (2023) recovered it as sister to the clade containing Scolioidea, Formicoidea and Apoidea; and finally Peters et al. (2017) recovered Vespoidea as sister to both of those clades (Figure 1, inset 5A/5B).

Except for Huang et al. (2019), who recovered a Middle Jurassic origin of the superfamily, the majority of node dating studies indicate that crown-group Vespoidea originated and diversified during the Early Cretaceous (144–109 Ma) (Blaimer et al., 2023; Peters et al., 2017; Wilson et al., 2013). According to Wilson et al. (2013) both Vespidae and Rhopalosomatidae originated in the Early Cretaceous (~120 Ma) (Table S2). The oldest fossil associated with Vespoidea is †*Priorvespa longiceps* Carpenter & Rasnitsyn from the Turga locality (~124 Ma), followed by several other †*Priorvespa* and †*Curiosivespa* species from the Bon Tsagaan and Baissa localities (~119 Ma). Perrard et al. (2017) pointed out that the position of †*Priorvespa* and †*Curiosivespa* relative to crown-group Vespidae is unclear, while Boudinot et al. (2022) recovered the two genera within crown-group Vespidae. If the two fossils are indeed members of crown-group Vespidae, both

Blaimer et al. (2023) and Wilson et al. (2013) estimates for the crown-group Vespoidea (109 and 120 Ma, respectively) would be too young.

Aculeata—Superfamily Formicoidea

The monophyly of Formicoidea and its sole constituent family Formicidae has never been seriously questioned and is fully supported by any genome-scale phylogenetic study (e.g., Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Peters et al., 2017). The sister group relationship of Formicoidea to Apoidea, however, was established more recently and together forms Formicapoidina. Formicapoidina is recognized by two synapomorphies: (1) the presence of longitudinal mesopectal sulcus and (2) having the fore wing crossvein 1cu-a anterior junction proximal to the branching point of M + Cu (Boudinot et al., 2022). Both molecular multi-locus studies (Debevec et al., 2012; Pilgrim et al., 2008; Wilson et al., 2013) and morphological studies (e.g., Brothers, 1999) found various relationships, including a sister group relationship to a clade comprising Apoidea + Scolioidea, as sister group to Scolioidea, or as sister group to a clade comprising Vespidae + Scolioidea. The sister group relationship of Formicoidea to Apoidea was first convincingly demonstrated in the phylogenomic study of Johnson et al. (2013) and was subsequently confirmed by all of the large-scale UCE and transcriptome studies on Hymenoptera (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Peters et al., 2017). The phylogeny of ants has been studied using various genetic data, ranging from single genes, UCEs and mitogenomes, to BUSCOs (e.g., Allio et al., 2020; Branstetter, Longino, et al., 2017; Romiguier et al., 2022). Many subfamilies and genera have received comprehensive treatments using UCE sequence data (e.g., Blaimer et al., 2015, 2018; Borowiec, 2019; Borowiec, Cover, & Rabeling, 2021; Camacho et al., 2022; Ješovnik et al., 2017; Prebus, 2017; van Elst et al., 2021; Williams et al., 2020).

The age of crown-group Formicidae has been estimated from the Early Cretaceous (130–118 Ma) (Boudinot et al., 2022; Branstetter, Danforth, et al., 2017) to the Late Cretaceous (90 Ma) (Wilson et al., 2013) (Table S2). The oldest fossils associated with Formicoidea are several Formicidae fossils from the Early–Late Cretaceous Charentese (~102 Ma) and Taimyr amber (~99 Ma), followed by more than 50 Formicidae fossils from the Burmese amber (~97 Ma). These fossils are most likely stem Formicidae. Barden (2017) summarized and reviewed the fossil record of ants, concluding that †*Kyromyrmex neffi* Grimaldi & Agosti from the Late Cretaceous New Jersey amber (~92 Ma), might be one of the oldest fossils clearly belonging to the crown-group Formicidae (Table S3c), which has been confirmed in the analysis of Boudinot et al. (2022). Boudinot et al. (2022) also recovered some undescribed species from Burmese amber (~97 Ma) within the crown-group, further suggesting that the Early Cretaceous origin for the crown-group might be more likely.

Aculeata—Superfamily Apoidea

Apoidea comprises the apoid wasps and the bees (Anthophila). The paraphyletic nature of the apoid wasps, traditionally often divided into

Ampulicidae, Crabronidae, Heterogynaidae and Sphecidae, was long suspected and proven multiple times using multi-locus and genomic data. This situation was recently addressed by Sann et al. (2018, 2021) using a combination of transcriptome and target enrichment data, by elevating a number of previously lower level groupings to family status. According to Sann et al. (2018, 2021), the apoid wasps now comprise 12 separate families: Ammoplanidae, Astatidae, Bembicidae, Crabronidae, Entomosericidae, Eremiaspheciidae, Heterogynaidae, Mellinidae, Pemphredonidae, Philanthidae, Psenidae and Sphecidae. These findings are at least partially supported by other phylogenomic studies, albeit with less comprehensive taxonomic sampling (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Peters et al., 2017), and especially the phylogenetic position of the newly erected families Entomosericidae and Eremiaspheciidae remains to be established (Sann et al., 2021). Further, discrepancies persist in the phylogenetic placement of Heterogynaidae, which was recovered controversially within Bembicidae in Sann et al. (2018). Upon reanalysis, Sann et al. (2021) recovered Heterogynaidae as the sister group to Mellinidae, which together form the sister group to the redefined Sphecidae + Crabronidae, a topology consistent with other published research (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017).

The Anthophila (bees) is another group that has been extensively studied using different phylogenomic data, ranging from transcriptomes, UCEs, to low-coverage genomes (Almeida et al., 2023; Bossert et al., 2019, 2022; Orr et al., 2022). The higher level relationships among the bee families have been consistently found as displayed in Figure 1 using phylogenomic data from different sources. Like for ants, extensive phylogenomic work has been carried out to establish the phylogeny of various lower level groupings including subfamilies and genera (e.g., Bossert et al., 2020, 2021; Branstetter et al., 2021; Freitas et al., 2021, 2023; Gueuning et al., 2020; Odanaka et al., 2022; Sandoval-Arango et al., 2023; Zhang, Niu, et al., 2022).

The age of Apoidea has been inferred in most of the dating studies that addressed Hymenoptera. Estimates for the crown-group Apoidea vary significantly across different analyses, from the Early–Late Jurassic (185–153 Ma) (Peters et al., 2017; Sann et al., 2018) to the Early–Late Cretaceous (131–102 Ma) (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Wilson et al., 2013). According to the dating studies, most of the Apoidea families seem to have originated during the Early Cretaceous (Bossert et al., 2022; Branstetter, Danforth, et al., 2017; Cardinal & Danforth, 2013; Cardinal et al., 2018; Gonzalez et al., 2019; Peters et al., 2017; Sann et al., 2018); however, age estimates sometimes vary significantly between different analyses and studies. For example, the origin of crown-group Andrenidae was estimated from the Late Cretaceous (~90 Ma) (Bossert et al., 2022; Cardinal & Danforth, 2013) to the Late Cretaceous to Paleocene boundary (~65 Ma) (Cardinal et al., 2018). The origin of Anthophila has been estimated to the Early Cretaceous (~125–115 Ma) (Almeida et al., 2023; Cardinal & Danforth, 2013; Sann et al., 2018) (Table S2). A comprehensive summary of all major dating analyses on bee divergence times is presented in Almeida et al. (2023).

Additionally, there are several dating studies on lower taxonomic levels. Gibbs et al. (2012) estimated ages for crown-group lineages of halictid bees and the origin of eusociality to the latest Eocene

(~35 Ma). Hines (2008) provided an age estimate for the diversification of extant bumble bee lineages to Eocene (40–25 Ma). Rehan et al. (2013) estimated the diversification of Xylocopinae to the Early to Late Cretaceous. Within the total-evidence tip dating framework, Gonzalez et al. (2019) estimated the origin of the leaf-cutter bees to mid-Oligocene to early Miocene (25–15 Ma) and Gonçalves et al. (2022) estimated the origin of Augochlorini to the Paleocene (~62 Ma).

The Cretaceous estimates for the crown-group Apoidea are clearly too young given the two oldest fossils associated with Apoidea from the Early Cretaceous Lulworth Formation (~143 Ma), †*Pompilopterus wimbledonix* Rasnitsyn et al. and †*Pompilopterus difficilis* Rasnitsyn et al. However, their placement within the superfamily was found dubious in the phylogenetic analysis by Boudinot et al. (2022), and they are instead recovered as the oldest Vespaculeata (Aculeata without traditional Chrysoidea). According to the same study, †*Angarosphex penyalveri*, Rasnitsyn & Martínez-Delclòs from the Early Cretaceous of Mongolia (~127 Ma) is the oldest definite Apoidea fossil (Table S3c), making an Early Cretaceous origin of crown-group Apoidea still feasible. The late Early Cretaceous age estimates for crown-group Anthophila seem reasonable given the oldest undisputable bee fossil, †*Cretotrigona prisca* (Michener & Grimaldi), from the Late Cretaceous New Jersey amber (~68 Ma).

A PERSPECTIVE ON FUTURE INROADS INTO HYMENOPTERA TAXONOMY AND SYSTEMATICS

Resolving the Hymenoptera bush of life

With the rapid advances in sequencing technology, there is a significant increase in the scale of Hymenoptera phylogenomic studies, both in terms of the number of markers and taxa. However, despite these advances, there is a lack of consensus on the deep backbone phylogeny between phylogenomic studies. The first two large-scale Hymenoptera phylogenomic studies—(1) the Peters et al. (2017) transcriptome study, which incorporated 3256 protein-coding genes from 173 taxa; (2) and the Branstetter, Danforth, et al. (2017) UCE study, which included 854 UCE loci from 187 taxa—both had somewhat limited taxon sampling, with a bias towards Aculeata and under-sampling of parasitic wasps. The Blaimer et al. (2023) study is the most comprehensively sampled to date, with 771 taxa and upwards of 447–1118 UCE loci from most known families. The higher level relationships within Blaimer et al. (2023) were also mostly corroborated by earlier morphological and molecular data. Subsequent UCE studies which have focused on densely sampling certain groups such as Chalcidoidea (Cruaud et al., 2024) and Symphyta (Wutke et al., 2024) have largely agreed with the Blaimer et al. (2023) study, albeit, not surprisingly, with much better resolution among the families. Therefore, the Blaimer et al. (2023) phylogeny is the base of our preferred tree (Figure 1), with some small refinement from other studies to improve relationships among families (Cruaud et al., 2024; Sann et al., 2021; Wutke et al., 2024).

With the development of sequencing technologies, high-quality Hymenoptera genomes generated using second (short-read) or third-generation (long-read) sequencing technologies are being published at an exponential rate (Branstetter et al., 2018; Hotaling et al., 2021). While the taxonomic focus is still skewed towards certain taxa like bees and ants, efforts of sequencing the lesser known 'dark taxa' are also on the way, with regional projects such as the Darwin Tree of Life for the UK, and European Reference Genome Atlas for European Union. The low input DNA from small specimens still provides a challenge to generating high-quality genomes, but a potential solution could be using whole genome amplification to increase yield, as demonstrated by Cruaud et al. (2018) on a single *Trichogramma* specimen. Recently, a new species of gall wasp was even described along with its genome (Brandão-Dias et al., 2022), providing a new gold standard for taxonomic vouchers. More studies are also using BUSCO genes (Simão et al., 2015), often in conjunction with UCEs or mitogenomes from either published genomes or newly sequenced low-coverage whole-genomes (Zhang, Niu, et al., 2022). So far, this method has largely been used within sawflies (Herrig et al., 2024), gall wasps (Hearn et al., 2024), bees (Orr et al., 2022; Zhang, Niu, et al., 2022) and ants (Romiguier et al., 2022), where more published genomes are available or there are ongoing initiatives to sequence whole genomes. With the push and active development of standardized nuclear markers across Metazoa (Dietz et al., 2022, 2024; Eberle et al., 2020), we suspect that this strategy will become the dominant approach in the upcoming years.

Simply increasing the number of molecular markers will not effectively resolve every problematic node in the Tree of Life (reviewed in Kapli et al., 2020; Steenwyk et al., 2023; Tihelka et al., 2021; Young & Gillung, 2020). Confounding factors such as orthology prediction, missing data along with compositional, rate and gene tree heterogeneity can lead to analytical errors, and therefore the detection of these potential sources of error is needed for downstream analyses (Du et al., 2023; Kapli et al., 2020; Steenwyk et al., 2023; Young & Gillung, 2020). Thorough analyses using multiple matrices with various levels of completeness, selecting more complex but computationally expensive evolutionary models, more stringent filtering of loci or groups, and use of coalescent approaches are just some of the current best-practices. While this can be overwhelming to researchers not familiar with the literature on the ever-increasing programmes and best practices of phylogenomics, there are excellent tutorials and custom scripts available to automate the process of multiple sequence alignment, trimming and loci filtering (e.g., Du et al., 2023; Steenwyk et al., 2021). An exciting emerging phylogenomic method is utilizing synteny (the conserved collinearity of orthologous loci from highly contiguous genome assemblies), which can be further divided into microsynteny (local gene orders) or macrosynteny (chromosomal organization), to resolve the deep and recalcitrant nodes across the animal tree of life (reviewed in Steenwyk & King, 2024). These methods can be used as an independent line of evidence to test the problems that we have highlighted within the Hymenoptera phylogeny and can be used to easily identify paralogs thus improving the accuracy of downstream analyses. However, it is still premature to know if these

methods will resolve the rapid and dense radiation observed in mega-diverse lineages of Hymenoptera such as Ichneumonoidea and Chalcidoidea.

While our understanding of the higher level relationships of Hymenoptera is being progressively refined, significant work remains to capture the true species diversity of extant Hymenoptera. Several hyperdiverse lineages of Hymenoptera remain understudied and can safely be considered 'dark taxa' (Srivathsan et al., 2023). In addition to the five recalcitrant nodes that we highlighted in the phylogenetic overview of Figure 1, in-depth studies for many superfamilies (e.g., Diaprioidea, Proctotrupeoidea and Ceraphronoidea) are needed to determine the validity of current family/generic level limits, ideally in conjunction with morphological data for a comprehensive treatment of extant and extinct taxa. Automation of time-consuming steps in the discovery and description of new taxa, potentially based on the mitochondrial fragment *COI*/DNA barcoding, has significant potential to dramatically expedite this process, and its implementation is an active topic of research (e.g., Hartop et al., 2022; Srivathsan et al., 2021). However, animal mitochondrial loci such as *COI* can also lead to an overestimation of the number of species, as they have higher mutation rates, lower effective population size and little to no recombination when compared with nuclear DNA, which can be further exacerbated by reduced gene flow, introgression and endosymbiont infection by *Wolbachia* (Eberle et al., 2020). As an alternative, Eberle et al. (2020) suggested the use of BUSCO genes (Simão et al., 2015) as an extension to DNA barcoding in future studies including Hymenoptera. To this end, they have identified 854 BUSCO candidates that seem specific to the order. A potentially cost-effective solution could be the simultaneous generation of multiple long-read loci (mitochondrial and nuclear) using third-generation sequencing techniques such as ONT MinION. In any case, methods involving the 'fishing' of legacy markers (genes used in traditional Sanger sequencing approaches) from genomes or raw targeted capture sequences, or the 'Frankenstein tree' method of building robust backbones using phylogenomic level data and integrating it with taxon-dense sampling of legacy markers, is becoming increasingly popular (e.g., Branstetter & Longino, 2019; Santos & Brady, 2024). It is also noteworthy that the majority of contemporary phylogenomic research is predominantly centered in the Global North, which often holds extensive museum samples owing to historical colonial influences. To rectify this geographical bias and ensure a more equitable representation, prioritizing the taxonomic sampling of the remarkably diverse fauna of the Southern Hemisphere is critical. This undertaking, however, should be executed collaboratively with local scientists to foster inclusivity and uphold principles of equity in future scientific exploration.

Towards more consistent and reliable age estimates

Our review highlights the huge variation in divergence age estimates for Hymenoptera and constituent lineages, as a result of applied divergence dating methods and calibration points, as well as taxon sampling and recovered tree topology. For example, the age

estimates for the nodes of interest (Figure 2) from the four higher level phylogenomics studies on Hymenoptera, which applied node dating (Blaimer et al., 2023; Branstetter, Danforth, et al., 2017; Peters et al., 2017; Tang et al., 2019) either considerably overlap (e.g., Apocrita and Tenthredinoidea) or barely overlap (e.g., Aculeata and Vespina). This discrepancy might be explained by the largely different calibration points across these studies (Table S4). Furthermore, both the choice of the root node prior, data set (amino-acid versus nucleotide) or relaxed-clock model (independent versus correlated rates) could have influenced the age estimates as demonstrated by the sensitivity analyses performed in these four studies and supported by findings of Warnock et al. (2012) and Kittel et al. (2016). The numerous age estimates for the crown-group Hymenoptera further emphasize the impact of the dating approach. On average, the estimates coming from tip dating studies are older than the estimates coming from node-dating studies. Among the tip dating studies, those employing uniform tree prior or mis-specifying taxon sampling strategy under the FBD prior produced older age estimates. These observations are not unique for Hymenoptera datasets and have been reported for other organisms (e.g., Arcila et al., 2015; Herrera & Dávalos, 2016; Simões et al., 2020).

While the node dating approach still dominates in empirical dating studies, the prevalent opinion in the field of divergence dating is that tip dating under fossilized birth-death models is a way forward in obtaining more informed and comprehensive age estimates. However, the performance of these models relies on several factors: (i) the sensible sampling of fossils (Matschiner, 2019; O'Reilly & Donoghue, 2020) and their correct placement in the phylogeny (but see Mongiardino Koch et al., 2023), (ii) prior information on the extant diversity of the group of interest (Gavryushkina et al., 2014; Zhang et al., 2016, 2023) and (iii) more realistic modelling of the fossilization process, uncertainty in the age of fossils (Barido-Sottani et al., 2019; Püschel et al., 2020), taxon sampling (Luo et al., 2023), and in the case of total-evidence datasets, morphological evolution (Lewis, 2001; Simões et al., 2020; Tarasov, 2023; Wright et al., 2016). Hymenoptera are both megadiverse and poorly known, both in terms of their extant and fossil diversity. This poses significant challenges to various aspects of divergence dating in the context of the FBD prior, especially regarding the fossil sampling and establishment of informative priors on the model parameters.

Although there are currently around 6000 Hymenoptera fossils belonging to almost all known superfamilies (PaleoBioDB, 2024), the fossil record and the described fossil species diversity are unevenly distributed across different groups, with about 1/3 of the described fossils belonging to Formicoidea, while 45 extant Hymenoptera families have none, and 27 extant Hymenoptera families (many belonging to Chalcidoidea) have a single fossil representative (Table S3a). In addition, around 50% of the described Hymenoptera fossils has been described in the 19th and 20th centuries and urgently require modern reinterpretation and taxonomic revision given the wealth of taxonomic change in the classification of many groups that followed the initial fossil descriptions (e.g., Ichneumonoidea and Chalcidoidea). This is of particular relevance for providing credible calibration points.

While the unresolved FBD tip dating approach can accommodate some of the uncertainty in the fossil placement, the more objective placement of fossils in a phylogeny can only be done using a total-evidence dating approach, which requires careful examination and interpretation of morphological evidence and time-consuming establishment of morphological matrices.

On the bright side, the development of the dating approaches has sparked great interest for studying the fossil record of Hymenoptera among neontologists, who in contrast to paleontologists, aim at understanding the evolution and ecology of extant taxa. The increase in collaborations between neontologists and paleontologists is speeding up the rates of fossil discovery and descriptions and providing more integrative approaches for fossil descriptions, thus reconciling evidence for reconstructing the evolutionary history of Hymenoptera. In 1975 and 2014, record numbers of 147 and 148 fossil species, respectively, have been described, and since 2018, more than 10 new extinct families of Hymenoptera have been established, mostly from the enigmatic ~100 million years old Burmese amber deposits (Tables S1b and S3; e.g., Jouault et al., 2021; Li et al., 2020; Melo & Lucena, 2019; Rasnitsyn et al., 2019; Rosa & Melo, 2023; Burmese Hymenoptera fauna is reviewed in Zhang et al., 2018). Moreover, there have been several recently published major revisions of the fossil record of specific hymenopteran groups, such as Ampulicidae (Ohl, 2004), Bethylinae (Ramos et al., 2014), Chrysoidea (Olmi et al., 2010), Cynipoidea (Pujade-Villar & Peñalver, 2019), Cretaceous non-aculeate Hymenoptera (Rasnitsyn & Öhm-Kühnle, 2021), Formicidae (Barden, 2017), Ichneumonidae (Spasojevic et al., 2018, 2022; Dehon et al., 2019; Viertler et al., 2022), Pompilidae (Rodriguez et al., 2017), Cretaceous Proctotrupomorpha (Rasnitsyn & Öhm-Kühnle, 2019) and Stephanidae (Ge et al., 2023). Several studies have also demonstrated the power of integrative approaches that combine classic study of fossil morphology with a total-evidence analysis (Klopfstein & Spasojevic, 2019; Meier et al., 2022) or morphometric analysis of wings (De Meulemeester et al., 2012; Li et al., 2019; Shih et al., 2020; Viertler et al., 2022) to help infer the placement of Hymenoptera fossils relative to presently known taxa.

Furthermore, both the interpretation of fossils and the creation of morphological matrices have been facilitated by technological advances to study morphology (reviewed in Wipfler et al., 2016). In particular, micro-CT has increasingly been used for non-destructive anatomical examination, species descriptions and taxonomic placement of both extant (e.g., Hita Garcia et al., 2017; Pasandideh Saqalaksari et al., 2020; Sarnat et al., 2019; van de Kamp et al., 2022) and extinct Hymenoptera (e.g., Boudinot et al., 2022; Bremer et al., 2021; van de Kamp et al., 2018; Viertler et al., 2023). Very few comprehensive morphological examinations across Hymenoptera have been published in recent years (but see Ronquist et al., 1999; Schulmeister, 2003; Vilhelmsen, 2001; Vilhelmsen et al., 2010), and this could partly be attributed to the lack of unified morphological terminology across the order or even within families, which can negatively impact studies on descriptive taxonomy, comparative phylogenetics, gene expression patterns, phenotype variability and machine learning algorithms (Dal Pos et al., 2023; Yoder et al., 2010).

The Hymenoptera Anatomy Ontology (HAO, Yoder et al., 2010) was developed in order to standardize morphological data in an ontological framework, and while it is in need of updates in light of recent advances in the field (e.g., Boudinot, 2018; Dal Pos et al., 2023; Girón et al., 2023), it remains an essential tool that is widely used by hymenopterists. By combining state-of-the-art morphological techniques with topological guidance from phylogenomic data, the need for a comprehensive re-examination of the morphology and anatomy across Hymenoptera is more pressing than ever.

Finally, to adequately use the FBD models, one will also have to carefully consider the prior knowledge on the extant diversity, as both the assumptions made about taxon sampling strategy (random versus diversified) and the proportion of sampled species can seriously impact the age estimates (e.g., Zhang et al., 2016). The studies within Hymenoptera that applied the FBD models usually fixed the sampling proportion of extant taxa relative to the current number of described species for the target group (e.g., see Gonzalez et al., 2019; Jouault et al., 2022; Lucena & Almeida, 2022; Zhang et al., 2023). These numbers are often far below the estimated true diversity of respective groups, as demonstrated for Hymenoptera, where the number of described species is at least 10 times smaller than the number of estimated species. Moreover, we lack credible estimates of species richness and taxonomists to power biodiversity discovery and descriptions for many Hymenoptera groups. However, the recently-established funds (e.g., ARTS and PurSUIT programmes of the U.S. National Science Foundation, European joint program Biodiversa+) and pipelines that aim at accelerating species discovery and descriptions through integrative taxonomic approaches (e.g., Hartop et al., 2022), together with more conscious and elaborate approaches for biodiversity estimation (Engemann et al., 2015; Li & Wiens, 2023; Stork et al., 2015), might give us more accurate estimates of Hymenoptera diversity in the future.

Open questions in Hymenoptera research

The decreasing cost associated with generating extensive phylogenomic data at large scales has spurred a notable surge in studies within the order Hymenoptera, confirming or contrasting morphology-based studies, establishing new hypotheses and identifying areas of uncertainties. To this date, there are several challenging nodes for which topologies are inconsistent across phylogenomic methods, often accompanied by relatively low nodal support. This lack of phylogenetic resolution despite the application of genome-scale information is not unique to Hymenoptera and is observed across other insects and beyond (Tihelka et al., 2021). This is not surprising given analytical limitations of phylogenetic methods and the complexity of the evolutionary process and necessitates meticulous curation and analysis to address the systematic errors associated with large datasets, such as missing data, paralogy, heterogeneous amino acid substitution and incomplete lineage sorting. It is imperative to provide detailed records of the analysis, including information (preferably fully reproducible) on contig assembly, orthology detection and model

specifications, and to deposit raw data and resulting trees as supplemental data when publishing these results. Such practices ensure repeatability and are integral to the scientific process, especially considering that subsequent macroevolutionary analyses like the study of historical biogeography or diversification rates can lead to vastly different conclusions based on potentially erroneous tree topologies. To enhance compatibility between different studies, especially when dealing with higher level phylogenies, the use of universal markers such as Hymenoptera-wide UCEs and Metazoa-wide BUSCO is needed to ensure a unified framework across studies. The gold standard for future genomic studies should involve the generation of high-quality genomes, enabling the bioinformatic extraction of various marker types, and thorough analyses accounting for phylogenetic heterogeneity. The employment of computationally expensive amino acid mixture models or synteny-based methods may aid in resolving recalcitrant nodes, and megadiverse lineages.

Although we have come a long way in understanding the time scale of Hymenoptera evolution, there is still uncertainty associated with the current Permian age estimate for crown-group Hymenoptera (~280 Ma) (Zhang et al., 2023). In addition, most hymenopteran lineages await age estimates from total-evidence tip dating studies that incorporate comprehensive sampling of extant and fossil taxa with the latest FBD models, to potentially reconcile the available node dating estimates often spanning several geological epochs. Improved divergence dates across Hymenoptera, but also across other insect groups, will help us further comprehend the extent of host-parasitoid co-diversification and the role of host-shifts in the evolution of the species-rich parasitoid lineages (Labandeira & Li, 2021). Finally, with the timeline of the angiosperm origin and diversification still being scrutinized (Salomo et al., 2017; Soltis et al., 2019; Zuntini et al., 2024), our understanding of the role of flowering plants in the diversification of insects, and in particular phytophagous and pollinating hymenopteran lineages, is constantly evolving in light of new evidence (Benton et al., 2022; Blaimer et al., 2023; Nyman et al., 2019; Peris & Condamine, 2024, van der Kooi & Ollerton, 2020; Vea & Grimaldi, 2016).

AUTHOR CONTRIBUTIONS

Y. Miles Zhang: Conceptualization; writing – original draft; writing – review and editing; data curation; validation; investigation; visualization; supervision; methodology; project administration. **Silas Bossert:** Investigation; writing – review and editing; visualization; validation; data curation; methodology. **Tamara Spasojevic:** Conceptualization; investigation; writing – original draft; writing – review and editing; validation; data curation; supervision; visualization; methodology.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The raw Newick version of Figure 1 is included in Supporting Information.

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SUPPORTING INFORMATION

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

Table S1. List of higher classifications of extant and extinct Hymenoptera.

Table S2. Overview of divergence dating studies and age estimates across Hymenoptera.

Table S3. Summary of the fossil record of Hymenoptera.

Table S4. Calibration points in the major large-scale node dating studies on Hymenoptera.

Data S1. Hymenoptera Phylogeny from Figure 1 in Newick format.

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