



Phylogenomics and biogeography of sawflies and woodwasps (Hymenoptera, Symphyta)

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ABSTRACT

Phylogenomic approaches have recently helped elucidate various insect relationships, but large-scale comprehensive analyses on relationships within sawflies and woodwasps are still lacking. Here, we infer the relationships and long-term biogeographic history of these hymenopteran groups using a large dataset of 354 UCE loci collected from 385 species that represent all major lineages. Early Hymenoptera started diversifying during the Early Triassic ~249 Ma and spread all over the ancient supercontinent Pangaea. We recovered Xyeloidea as a monophyletic sister group to other Hymenoptera and Pamphilioidea as sister to Unicalcarida. Within the diverse family Tenthredinidae, our taxonomically and geographically expanded taxon sampling highlights the non-monophyly of several traditionally defined subfamilies. In addition, the recent removal of *Athalia* and related genera from the Tenthredinidae into the separate family Athaliidae is supported. The deep historical biogeography of the group is characterised by independent dispersals and re-colonisations between the northern (Laurasia) and southern (Gondwana) palaeocontinents. The breakup of these landmasses led to ancient vicariance in several Gondwanan lineages, while interchange across the Northern Hemisphere has continued until the Recent. The little-studied African sawfly fauna is likewise a diverse mixture of groups with varying routes of colonization. Our results reveal interesting parallels in the evolution and biogeography of early hymenopterans and other ancient insect groups.

1. Introduction

With more than 153,000 species, the Hymenoptera constitutes one of

the largest and biologically most diverse insect orders (Aguilar et al., 2013; Forbes et al., 2018). Hymenopteran insects assume a huge variety of lifestyles, ranging from phytophagous to predatory and many forms of

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parasitoidism. This diversity of ecological niches makes hymenopterans a crucial part of almost all terrestrial ecosystems (Grimaldi and Engel, 2005). As pollinators, pests of cultivated plants and biological control agents, many species are also economically important (Grimaldi and Engel, 2005).

Traditionally, Hymenoptera are divided into the suborders “Symphyta” (sawflies and woodwasps) and Apocrita (parasitoid and predatory wasps, bees, and ants). The latter are characterised by the possession of a “wasp waist”—a characteristic constriction between the first and second abdominal segments—and make up the vast majority of all Hymenoptera (~144,000 species) (Aguilar et al., 2013). Apocrita are further divided into “Parasitica”, a paraphyletic group distinguished by their predominantly parasitoid lifestyle rather than any morphological characters, and the mainly predatory or pollinivorous Aculeata, whose ovipositor is modified into a stinger (Sharkey, 2007). In contrast, the “Symphyta” is a paraphyletic assemblage (Heraty et al., 2011; Klopstein et al., 2013; Malm and Nyman, 2015; Peters et al., 2017; Ronquist et al., 2012) of all non-apocritan lineages (approximately 9,000 described species (Taeger et al., 2018)), and is defined mainly based on the absence of a “wasp waist” (Fig. 1).

Recently, phylogenomic studies have helped clarify various apocritan relationships, such as for ants (Branstetter et al., 2017b; Mbanjana et al., 2024; van Elst et al., 2021), bees (Almeida et al., 2023; Bossert et al., 2019; Pisanty et al., 2021), and several groups of parasitoid wasps

(Blaimer et al., 2020; Cruaud et al., 2021; Santos et al., 2021). Many of these studies have relied on data generated by high-throughput sequencing of ultraconserved elements (UCEs), which are short, conserved genomic regions shared between distantly related taxa (Faircloth et al., 2012). While the core regions of UCE loci are highly conserved, their flanking regions are more variable, which makes UCEs suitable for resolving evolutionary relationships across widely varying timescales (Alfaro et al., 2018; Batista et al., 2020) and multiple taxonomic levels (Blaimer et al., 2023, 2020; Rasplus et al., 2020; Supeleto et al., 2020).

In contrast, equally comprehensive phylogenomic studies on relationships within “Symphyta” are still lacking. This is unfortunate because, along with Lepidoptera, Coleoptera, and Hemiptera, the symphytan grade constitutes one of the main radiations of plant-feeding insects (Grimaldi and Engel, 2005; Wiens et al., 2015). Despite recent advances in molecular and computational methods, there is still uncertainty surrounding the relationships and ages of many non-apocritan lineages (Blaimer et al., 2023; Malm and Nyman, 2015; Peters et al., 2017). For example, the placement and monophyly of the family Xyelidae, the superfamily Pamphilioidea (Megalodontesidae + Pamphiliidae), and the recently proposed family Athaliidae differ among studies (Blaimer et al., 2023; Klopstein et al., 2013; Malm and Nyman, 2015; Niu et al., 2022, 2021; Peters et al., 2017; Ronquist et al., 2012). Particularly relationships among, and ages of, families within the largest

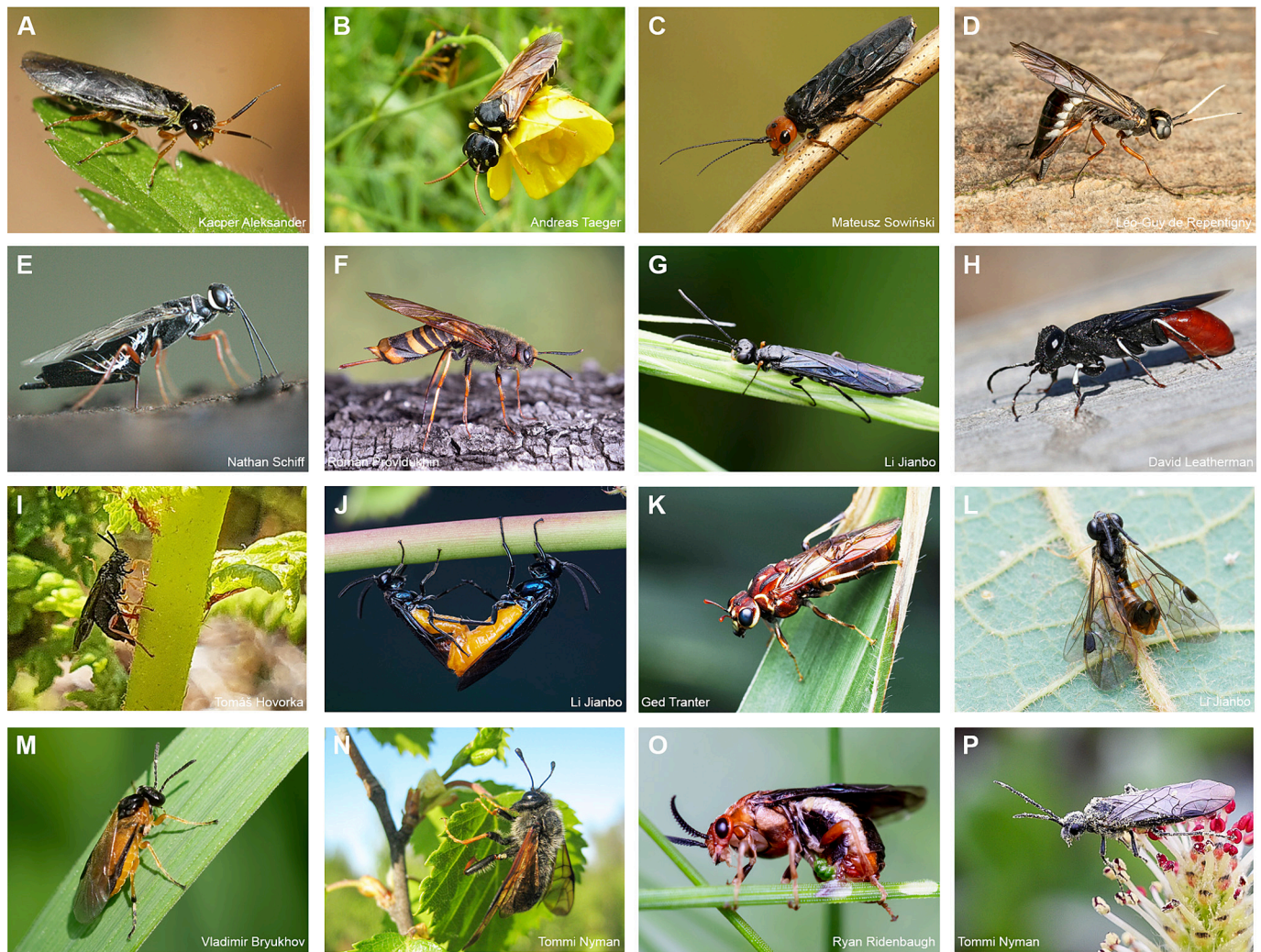


Fig. 1. Representatives of the 16 families of the symphytan grade of the Hymenoptera: (A) Xyelidae, (B) Megalodontesidae, (C) Pamphiliidae, (D) Xiphiidae, (E) Anaxyelidae, (F) Siricidae, (G) Cephidae, (H) Orussidae, (I) Blasticotomidae, (J) Argidae, (K) Pergidae, (L) Heptamelidae, (M) Athaliidae, (N) Cimbicidae, (G) Diprionidae, and (P) Tenthredinidae.

symphytan superfamily, Tenthredinoidea, remain largely unexplored with phylogenomic data.

Considerable uncertainty also exists regarding the long-term global biogeography of sawflies, because the topic has been addressed only for the families Orussidae (Vilhelmsen, 2004), Pergidae (Schmidt and Walter, 2014), Cimbicidae (Vilhelmsen, 2019), and Argidae (Malagón-Aldana et al., 2022). Although sawflies are found on all continents except Antarctica, the centres of diversity differ widely among the main symphytan taxa. Most symphytan families are currently distributed in temperate regions, while others can be found primarily in the Southern Hemisphere (Pergidae) (Schmidt and Smith, 2006) or worldwide (Tenthredinidae, Orussidae) (Taeger et al., 2018; Vilhelmsen, 2004). Therefore, even with a fossil record that dates back to the Late Triassic 235 million years ago (Ma) (Rasnitsyn and Quicke, 2002), we know little about the origin and biogeographic history of one of the major plant-feeding insect diversifications.

Here, we infer the evolutionary relationships and large-scale biogeographical patterns of symphytan lineages using a large dataset of 354 UCE loci collected from 385 species that represent all major groups of sawflies and woodwasps (Fig. 1). Our phylogenomic approach constitutes a large step forward from previous molecular studies, which have been based on many species but few genetic loci (Heraty et al., 2011; Klopstein et al., 2013; Malm and Nyman, 2015) or sequencing data from large parts of the genome sampled from few symphytan species (Michell et al., 2021; Niu et al., 2021; Peters et al., 2017; Tang et al., 2019). To expand the sampling of symphytan lineages to groups that are rare or occur in geographic regions that have been poorly represented in previous analyses, we took advantage of the fact that UCEs can be enriched from low-quality samples, such as pinned museum specimens (Blaimer et al., 2016; Faircloth et al., 2015). To elucidate the timing of the branching events near the root of the hymenopteran radiation and within the most diverse symphytan families, we time-calibrated our comprehensive phylogeny using 21 fossils. We then used the time-calibrated phylogeny to perform ancestral area reconstructions to infer the overall historical biogeography and dispersal patterns of sawflies. Our results provide new insights into the origin, diversification, and biogeography of early hymenopterans and provide a framework for future clade-specific analyses of the evolution of host-plant use, biogeography, and diversification dynamics within Hymenoptera.

2. Materials and methods

2.1. Taxon sampling, molecular methods, and data processing

Our dataset comprised 433 taxa, including 24 outgroup taxa representing 12 insect orders (Tables S1–S2). We sampled a total of 409 hymenopteran taxa, of which 385 represent sawfly species and 24 belong to the suborder Apocrita. The sampling covers all 16 extant sawfly families (Fig. 1) and 39 out of 42 subfamilies (Taeger et al., 2018), only lacking Dielocerinae (Argidae), Parasyzygoniinae and Styracotechyinae (both Pergidae). For all non-hymenopteran outgroups and apocritans, as well as for five sawfly taxa, we extracted UCEs from published genomes (Table S2). DNA was extracted from whole insects, single legs (for pinned specimens), or a piece of the abdomen (for ethanol-preserved specimens). We extracted genomic DNA using the DNeasy Blood and Tissue Kit (Qiagen) following the manufacturer's protocol. After assessing DNA concentration and quality on a Qubit 3.0 fluorometer (Thermo Fisher Scientific), we enzymatically fragmented the DNA for 20 min using NEBNext dsDNA Fragmentase (New England Biolabs). From the fragmented DNA, we constructed sequencing libraries with the NEBNext Ultra II DNA (New England Biolabs) library preparation kit following the manufacturer's instructions. This step included library barcoding with NEBNext® Multiplex Oligos (New England Biolabs). The final barcoded libraries were quantified on Qubit and pooled in batches of 6–8 libraries/pool at equimolar ratios. For UCE enrichment with myBaits UCE Hymenoptera 2.5Kv2P (Daicel Arbor Biosciences), we used

500 ng DNA of each pool and followed the myBaits protocol version 3.02 (July 2016) with on-bead amplification. The concentration of the enriched library pools was determined via qPCR using the NEBNext Library Quant Kit (New England Biolabs). The enriched pools were again pooled at equimolar ratios and sequenced on an Illumina HiSeq 2500 (150 bp paired end) at the Biomedicum Functional Genomics Unit (FuGU) in Helsinki (Finland).

For assembling, aligning, trimming and concatenating UCE loci across samples we followed the PHYLUC pipeline (Faircloth, 2016) with default settings unless otherwise stated. Demultiplexed FASTQ reads were trimmed using Illumiprocessor (Faircloth, 2013), a wrapper program for trimmomatic (Bolger et al., 2014), and assembled into contigs using Spades v3.13.0 (Bankevich et al., 2012). The Hymenoptera UCE probes were then matched to the assembled contigs at 70 % identity and 70 % coverage, and the extracted UCE loci were aligned using MAFFT 7.455 (Katoh and Standley, 2013) and internally trimmed with Gblocks 0.91b (Castresana, 2000; Talavera and Castresana, 2007). For genome-enabled taxa, we followed the PHYLUC pipeline for extracting UCE loci from the genome assemblies. For subsequent analyses, we selected a 75 % complete data matrix (data for at least 75 % of the 446 taxa) which resulted in a 40,004 bp long alignment and retained 354 UCE loci.

2.2. Phylogenomic analyses

2.2.1. Concatenated analyses

Phylogenomic estimations were conducted following concatenated and coalescent-based approaches. In the concatenated analyses, we reconstructed phylogenies by applying both maximum likelihood (ML) and Bayesian inference (BI) methods on the alignment of the 75 % complete matrix, i.e., based on loci present in at least 75 % of the taxa. We analyzed the data with and without partitioning by UCE locus. For the partitioned alignment, we determined the best-fitting partitioning scheme with PartitionFinder2 (Lanfear et al., 2017), applying the rclusterf algorithm (Lanfear et al., 2014), and the GTR + G model of substitution. Phylogenetic analyses on the unpartitioned and partitioned dataset using ML and BI methods resulted in four phylogenies for the concatenated alignments. We inferred the ML phylogenies using the MPI version of RAxML 8.2.12 (Stamatakis, 2014) with the rapid bootstrap algorithm (–f a) and 200 bootstrap replicates, assuming a GTRGAMMA site rate substitution model. The Bayesian phylogenies were estimated with the MPI hybrid variant of ExaBayes v. 1.5 (Aberer et al., 2014) with four independent runs, each having four coupled chains, running for 1 million iterations with default priors, sampling the trees every 500 generations. After discarding the first 25 % generations as burn-in, we assessed convergence of the posterior distribution visually in Tracer v. 1.7.1 (Rambaut et al., 2018) and checked for ESS > 200 (effective sample size). Additionally, we calculated the average deviation of split frequencies using the sdsf function included in the ExaBayes package. The consensus function from ExaBayes was used to generate consensus trees from the independent runs.

In order to explore the impact of missing data, substitution model selection, data partitioning, and heterogeneity on the phylogenetic trees, we also ran several additional analyses: (a) using RAxML on an unpartitioned data matrix with a higher amount of missing data (65 % complete matrix) but more UCE loci (705 loci, 83 kb), (b) using ModelFinder (Kalyaanamoorthy et al., 2017) implemented in the IQ-TREE software (Nguyen et al., 2015) to find the best-fitting substitution model and inferring a maximum-likelihood tree of the unpartitioned dataset with branch supports based on ultrafast bootstrap (Hoang et al., 2017), (c) employing the Sliding-Window Site Characteristics Entropy (SWSC-EN) algorithm (Tagliacollo and Lanfear, 2018) and PartitionFinder2 with above settings for data partitioning and ExaBayes as described above for phylogeny estimation, and (d) partitioning the alignment by UCE locus and excluding partitions that violate the assumptions of stationarity and homogeneity (Naser-Khdour et al., 2019)

from tree inference in IQ-TREE.

2.2.2. Coalescent-based analyses

Next, we constructed species trees under the multi-species coalescent (MSC) using ASTRAL-III (Zhang et al., 2018) and SVDQuartets (Chifman and Kubatko, 2014). The input for ASTRAL-III was a set of gene trees estimated from every UCE locus separately (same loci which were used to create the concatenated alignment, 354 gene trees). Individual gene trees were constructed in IQ-TREE v. 2.0.5 (Minh et al., 2020), including selection of the best substitution model (Kalyaanamoorthy et al., 2017), and branch support was measured as ASTRAL's local posterior probabilities. The SVDQuartets method implemented in PAUP* (Swofford, 2002), was used with the concatenated alignment as input. SVDQuartets estimates the best tree for each quartet of species in the dataset and constructs a species tree from all sampled quartet trees. We calculated branch support values by generating 100 bootstrap replicates.

Because the position of the root varied in the analyses including outgroup taxa, we also estimated the topology without an outgroup and used RootDigger v. 1.7.0 (Bettisworth and Stamatakis, 2021) to compute the root location.

2.2.3. Topology tests

Finally, we calculated likelihood scores for each rooted topology in IQ-TREE v. 2.0.5 (Minh et al., 2020), and selected the tree with the highest likelihood value. We compared the tree topologies from the various concatenated (two different partitioning schemes, each analyzed with both RAXML and ExaBayes) and coalescent-based analyses (using each UCE separately for ASTRAL and SVDQuartets), and several alternative topologies proposed in previous studies (Table S4). We computed the log-likelihood of each topology based on 10,000 RELI replicates and various topology tests implemented in IQ-TREE: bootstrap proportion (BP), Kishino-Hasegawa test (Kishino and Hasegawa, 1989), Shimodaira-Hasegawa test (Shimodaira and Hasegawa, 1999), expected likelihood weights (Strimmer and Rambaut, 2002), and approximately unbiased (AU) test (Shimodaira, 2002).

2.3. Data filtering and divergence-time estimation

To reduce computational burden, we used only subsets of the final 75 % complete dataset (without outgroups) for the divergence-dating analyses. These subsets were created by selecting: (a) the 25 % most parsimony-informative UCE loci, (b) the 25 % most clock-like loci and, (c) random subsets of 25 % of all UCE loci. Summary statistics, including the proportion of parsimony-informative sites and GC content, were calculated using the AMAS script (Borowiec, 2016). Filtering all 354 UCE loci for clock-likeness was conducted with the SortaDate package (Smith et al., 2018). Random subsets of UCE loci were created with the PHYLUCE script `phyluce_align_randomly_sample_and_concatenate`, each subset consisting of 88 loci. Previous studies have been ambiguous on the most reliable subsampling strategy—while some studies have found clock-like loci to be most informative (Smith et al., 2018), others have postulated that random loci perform better (Mongiardino Koch, 2021). Accordingly, divergence times are given as the mean of our subsampled datasets. Divergence dating was conducted in BEAST v2.6.3 (Bouckaert et al., 2014), using 21 fossil-based node calibrations and a fixed topology (Table S3). Fossils were chosen to represent the oldest available and reliable calibration for each symphytan superfamily and family, as well as two subfamilies, and some other crucial relationships. The calibrations were limited to these deeper nodes, as evidence suggests that calibration priors placed at deep phylogenetic nodes increase the precision and accuracy of divergence times (Mello and Schrago, 2014). As input tree, we used the unpartitioned ExaBayes topology, which was the topology with the highest likelihood, rooted with RootDigger. The substitution model was inferred during the analysis by employing the bModelTest package (Bouckaert and Drummond, 2017). We further used an uncorrelated relaxed lognormal clock model and birth-death

tree prior. Run convergence was analyzed with Tracer v1.7.1 (Rambaut et al., 2018) by verifying that the effective sample sizes (ESS) were > 200 for all estimated parameters. A maximum clade credibility (MCC) tree was summarized from the combined runs with LogCombiner v2.6.3 and TreeAnnotator v2.6.3 (both distributed with the BEAST package) after discarding the initial 10 % of trees as burn-in and subsampling 20 % of post-burnin trees. Additionally, we ran the program without data by sampling only from the prior to examine the informativeness of our sequence data and if the choice of priors was reasonable.

2.4. Ancestral range estimation

To infer the global biogeographical history of the symphytan lineages of the Hymenoptera, we estimated ancestral ranges using the R package BioGeoBEARS v1.1.1 (Matzke, 2018, 2013). As the input tree, we used a modified version of the time-calibrated MCC tree, which we pruned to include only samples that were determined to species level or for which the whole genus occurs in only one of the defined biogeographic areas (Table S4). We retrieved the information on present-day distribution for each species and genus from the Electronic World Catalog of Symphyta (ECatSym) (Taeger et al., 2018). This information was used to assign taxa to seven biogeographic areas: Palearctic (Eurasia north of the Himalayas, North Africa), Nearctic (North and Central America), Oriental (India and Southeast Asia), Neotropic (South America), Afrotropic (Sub-Saharan Africa and Madagascar), Australasia (Australia, New Zealand, and Melanesia), and Antarctica. Although there are no sawflies in Antarctica today, the Antarctic landmass most likely acted as a route for dispersal during Gondwanan times, when the global climate was warmer and the southern continents still remained connected (Schmidt and Walter, 2014). We tested three different models implemented in BioGeoBEARS: DEC (Dispersal-Extinction-Cladogenesis), DIVA-like (likelihood version of Dispersal-Vicariance Analysis DIVA), and BAYAREA-like (likelihood version of BayArea range evolution model). These models differ in the way areas are inherited along branches: all models allow dispersal and extinction, DEC allows narrow vicariance and narrow and subset sympatry, DIVA-like permits both narrow and wide vicariance and narrow sympatry, and BAYAREA-like does not permit range evolution during cladogenesis (descendants inherit the range occupied by their ancestor). Each model was further tested with and without the founder-event parameter (+J). Recently, the inclusion of founder-event speciation (+J) has been under discussion, as Ree and Sanmartín (2018) claimed that comparison of models with and without the 'J' parameter is not statistically valid and that the likelihood of cladogenetic events tends to be overestimated in '+J' models. However, Matzke (2022) validated the statistical model comparison. Therefore, we include both models with and without founder-event (+J) in our ancestral range estimations. Each model was first run without any constraints (referred to as M0) and, secondly, with constraints implementing time-stratified dispersal multipliers (referred to as M1, Table S5). Under M1 analyses, the dispersal probability differs between regions (1: directly connected regions; 0.5: connected via another region or "narrow" sea; 0.0000001: distant regions) and between time periods. Based on palaeogeographical reconstructions of plate tectonics corresponding to the connectivity between Gondwanan landmasses (Ali and Aitchison, 2008; Blakey, 2008; Scotese, 2016; Seton et al., 2012), we defined four time bins for the time-constrained M1 model: 0–50 Ma, 50–110 Ma, 110–170 Ma, and 170–300 Ma. We constrained the maximum number of areas allowed for each node to five.

To assess the impact of sampling bias on phylogeographic results, distribution data were changed to correspond roughly to current distribution ratios of sawfly species. These modified distribution matrices were produced by two strategies. Firstly, we discarded taxa from over-represented regions. However, this strategy was not possible for all families due to the lack of samples from some regions. To overcome this problem, we extended the distribution of certain taxa, so that the overall distribution of that family matched modern-day distribution ratios.

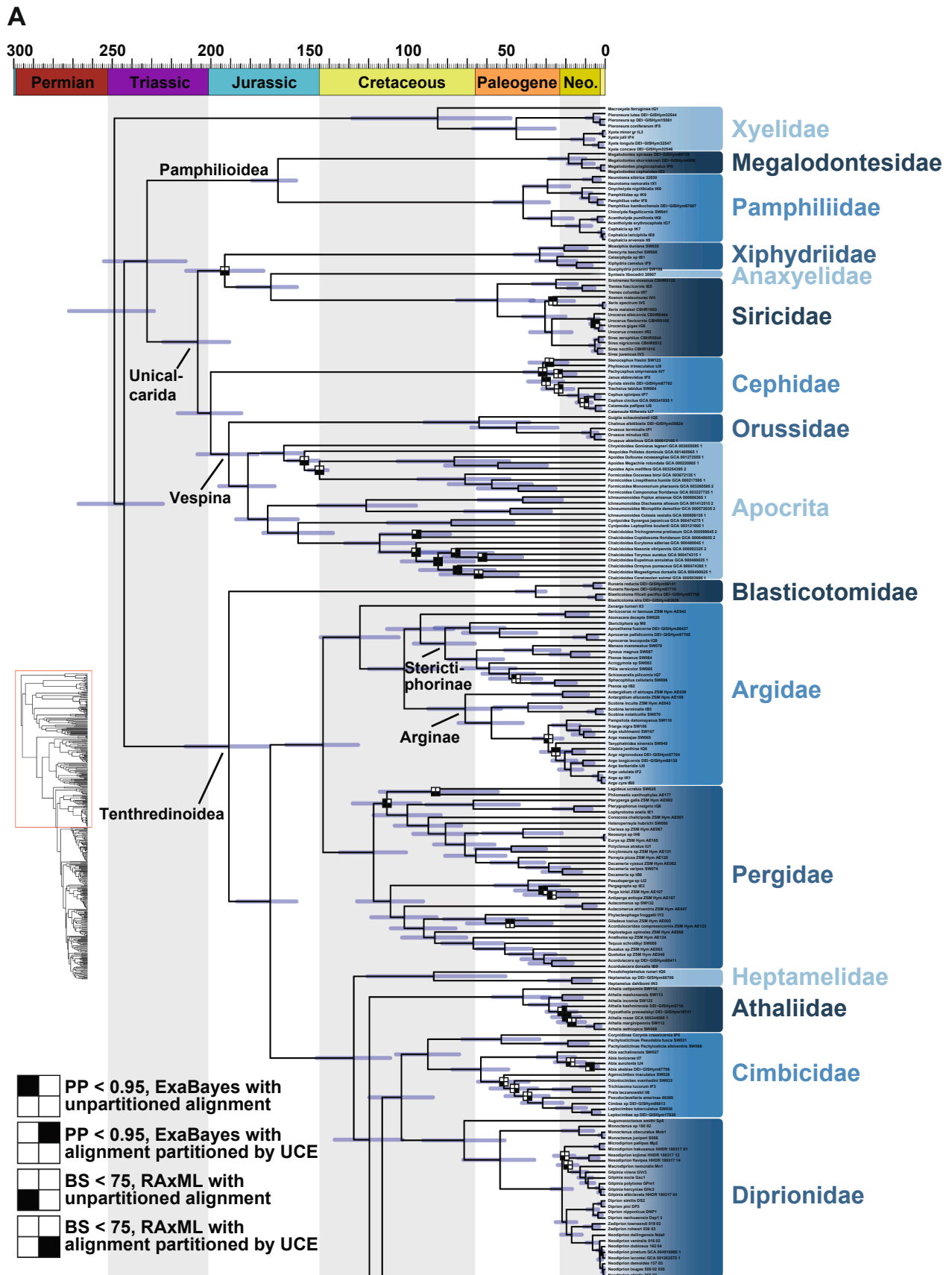
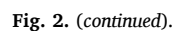


Fig. 2. Time-calibrated phylogeny of the Hymenoptera based on the best-fitting tree topology and 25% most clock-like UCE loci. (A) Non-tenthredinid sawfly families and the Apocrita, (B) the Tenthredinidae *s.str.* clade. Red squares in the inset trees delineate the locations of panels (A) and (B) on the full hymenopteran phylogeny. Blue bars on nodes show 95% HPD intervals of age estimates. Nodes without symbols indicate full clade support of 1.0 Bayesian posterior probability (PP) and 100% Maximum likelihood bootstrap support (BS), nodes receiving weak support in some of the analyses are indicated by black squares (see legend).



3. Results

3.1. Phylogenetic relationships and divergence-time estimates

The final dataset consisted of 354 UCE loci and had a total length of 40,004 bp. According to topology tests, the ExaBayes analysis of the unpartitioned alignment excluding non-hymenopteran outgroups resulted in the overall best topology (Fig. 2, Table S6). This topology of family-level relationships (Fig. 3A) was shared by all but one concatenated RootDigger-rooted analyses. The same family-level topology was also produced by the additional analyses exploring the effects of the amount of missing data, heterogeneity, model selection, and

partitioning scheme. The relationships differed between concatenated and coalescent-based analyses, but we consistently resolved all sawfly families as monophyletic among analyses (Figs. S1–S10). At the subfamily level, most clades were resolved with high support, but many morphologically defined subfamilies were not recovered as monophyletic: Monocteninae (Diprionidae), Xiphydriinae (Xiphydriidae), the two siricid subfamilies Siricinae and Tremicinae, and most of the tenthredinid subfamilies (Blennocampinae, Allantinae, Heterarthrinae, and Tenthredininae). Within Argidae, the subfamily Athermantinae came out polyphyletically inside Arginae, rendering the latter paraphyletic. We obtained different root locations in analyses including an outgroup, which also changed the position of Xyelidae (Figs. S1–S10). However,

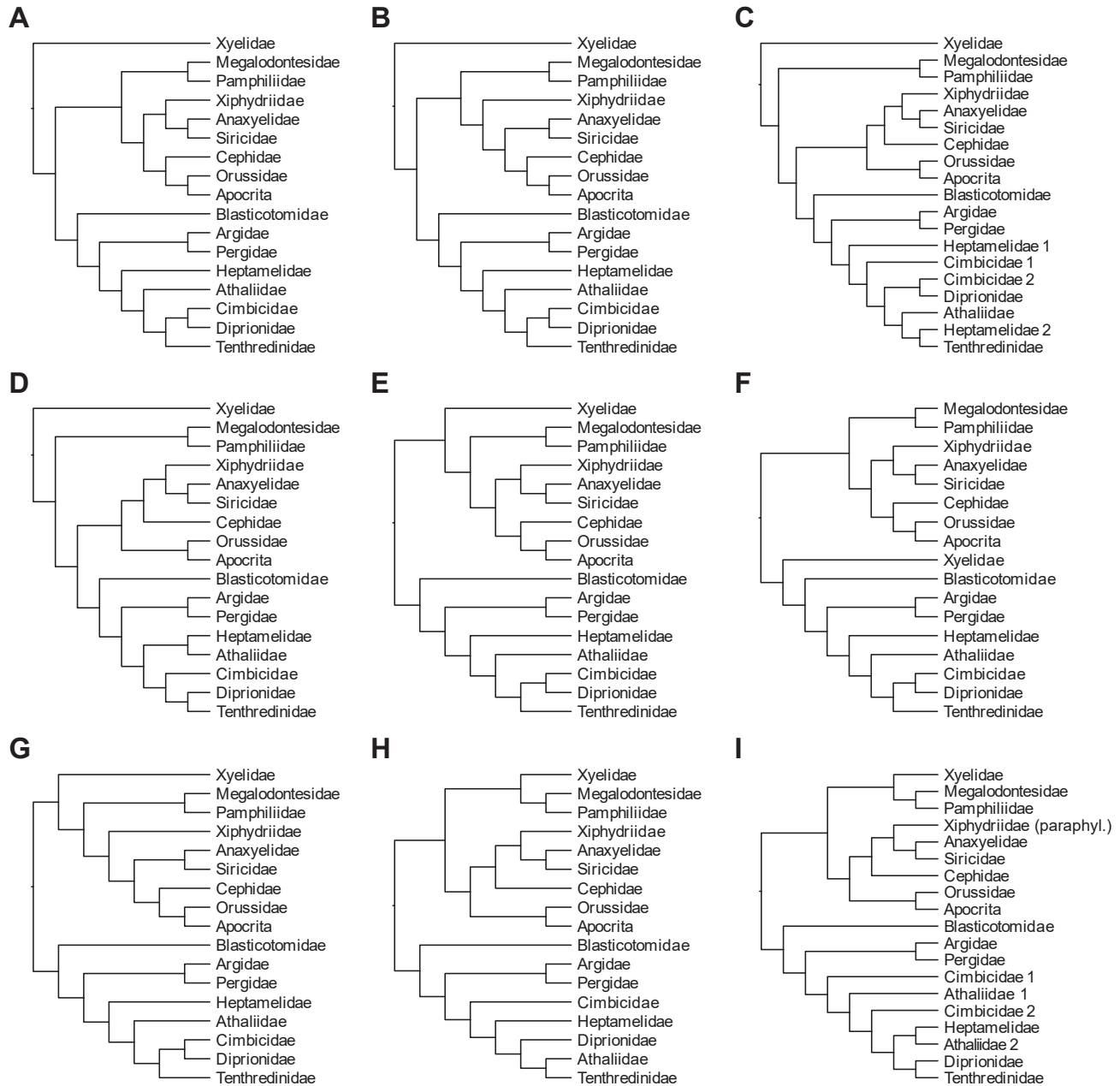


Fig. 3. Family-level summaries of topologies supported by different analyses in which trees were rooted either using RootDigger (A–D) or by including outgroups (E–I). (A) Main family-level topology, supported by unpartitioned and UCE-partitioned ExaBayes analyses, the unpartitioned RAXML analysis, and the four additional analyses exploring the impact of missing data, substitution model selection, data partitioning, and heterogeneity (RAXML analysis of the 65% complete matrix, IQTREE analysis employing model selection by ModelFinder, ExaBayes analysis partitioned using the SWSC-EN algorithm, and IQTREE analysis excluding “bad” UCE partitions). (B–I) Alternative topologies supported by (B) the UCE-partitioned RAXML analysis, (C) ASTRAL analysis, (D) SVDQuartets analysis, (E) unpartitioned ExaBayes and RAXML analyses, (F) UCE-partitioned ExaBayes analysis, (G) UCE-partitioned RAXML analysis, (H) ASTRAL analysis, and (I) SVDQuartets analysis.

Xyelidae was consistently recovered as a sister group to all other Hymenoptera in analyses without outgroup and rooted with RootDigger.

Estimates of divergence times were congruent between analyses for most nodes (Figs. S11–S13, Table S7). According to our analyses, the diversification of Hymenoptera started during the late Early Triassic or Late Permian circa 249 Ma (95 % HPD: 229–272 Ma) (Fig. 2). The Xyelidae crown age is estimated at 85 (48–128) Ma, with a long stem to the crown group. For Pamphilioidea, the most recent common ancestor (MRCA) was dated to 166 (156–179) Ma. This node splits into the families Megalodontesidae and Pamphiliidae, both of which have a long branch leading to their relatively young crown groups, 18 (10–28) Ma and 41 (28–56) Ma, respectively. However, concatenated (ExaBayes, RAxML) and coalescent-based (ASTRAL, SVDQuartets) analyses recovered slightly different Pamphilioidea relationships. Concatenated approaches recovered Pamphilioidea as sister to Unicalcarida, as opposed to coalescent analyses, in which Pamphilioidea were either sister to Xyelidae or diverged as their own clade right after the split of Xyelidae as sister to Tenthredinoidea + Unicalcarida. The parasitoid wasp family Orussidae was recovered as the sister to all Apocrita with a crown age of 64 (38–91) Ma. We estimated the beginning of the radiation of the superfamily Tenthredinoidea at around 191 (170–213) Ma. Within Tenthredinoidea, our analyses placed the clade formed by *Athalia* and *Hypsathalia* species (crown age 41 (28–57) Ma) well outside Tenthredinidae, as sister to the Tenthredinidae and Cimbicidae + Diprionidae clade.

3.2. Ancestral range estimation

Our biogeographic analyses favoured the time-stratified (M1) DEC + J model as the best-fitting model (Table S8, Figs. S14–S15), but the time-stratified DEC model without ‘J’ recovered consistent results. The BAYAREA-like model was the least favoured, both with and without ‘J’. The ancestral range estimation yielded similar probabilities for each region i.e., a Pangaeian distribution for the hymenopteran MRCA (Fig. 4). Yet, the estimated ranges for the ancestors of the major clades differ. The most likely ancestral area of Xyelidae and other non-tenthredinoid families comprises primarily the Northern Hemisphere. Within the non-Tenthredinoidea clade, we nevertheless estimated a worldwide distribution for the MRCA of Orussidae and a Gondwanan origin for the MRCA of Xiphydriidae. After the breakup of Gondwana, Xiphydriidae continued to radiate in Australasia and the Neotropics. The ancestors of the xiphydriid sister clade, which involves the families Siricidae and Anaxyelidae, inhabited a Nearctic ancestral area, according to our reconstructions.

Unlike non-tenthredinoid families, the Tenthredinoidea dispersed globally but, after the Pangaeian supercontinent separated, the ancestral range of several families within this clade (Cimbicidae, Diprionidae, Tenthredinidae) was restricted to the Northern Hemisphere. However, the MRCA of the Argidae + Pergidae clade has a Gondwanan origin, the signature of which is retained by both families. For Pergidae, we reconstructed an ancestral area comprising Australia and the Neotropics. For their sister family Argidae, the ancestral area also included the Afrotropics. Within Argidae, the MRCA of the subfamily Arginae has an estimated ancestral area comprising tropical regions, but the MRCA of the subfamily Sterictiphorinae was distributed in the Nearctic, Palearctic, and Neotropics. The rapid diversification of Tenthredinidae started during the Cretaceous in the Palearctic around 142 (99–131) Ma. Most of the MRCAs of tenthredinid subfamilies remained in this ancestral area, but dispersal to the Neotropics, Southeast Asia, or Africa occurred several times independently.

4. Discussion

4.1. Phylogenetic relationships and divergence-time estimates

Our study aimed at resolving the timing, relationships, and

biogeographical patterns of the evolution of sawflies and woodwasps based on a large phylogenomic dataset involving sequence data from 354 UCE loci from 385 species representing all main groups of the symphytan grade of the Hymenoptera. We estimated the onset of the Hymenoptera diversification to the late Early Triassic or Late Permian (~249 Ma). These results are consistent with previous estimates (Branstetter et al., 2017a; Misof et al., 2014) and the fossil record, which dates the earliest hymenopteran fossils to the Late Triassic (235 Ma) (Rasnitsyn and Quicke, 2002). However, a few other recent studies have estimated an older Hymenoptera crown age (Nyman et al., 2019; Peters et al., 2017; Ronquist et al., 2012; Tang et al., 2019). There is particular discrepancy with the studies of Peters et al. (2017) and Blaimer et al. (2023) both of which were based on large molecular datasets (transcriptomes and UCE's, respectively) but also were very Apocrita-heavy with respect to taxon sampling. In the case of both studies, our results disagree not only for the crown-age estimate but also for the deep branching patterns among symphytan superfamilies. This is especially the case for the monophyly of Peters et al.'s Eusymphyta (=Pamphilioidea + (Tenthredinoidea + Xyeloidea)), and Blaimer et al.'s grouping of Tenthredinoidea as sister to all remaining Hymenoptera. However, Eusymphyta is a very unusual grouping that has not been retrieved in other studies. Instead, we recovered Xyeloidea as sister to other Hymenoptera, a relationship supported by most previous analyses with better representation of the main sawfly taxa (Heraty et al., 2011; Klopstein et al., 2013; Malm and Nyman, 2015; Ronquist et al., 2012; Sharkey et al., 2012) and Pamphilioidea as sister to Unicalcarida (see below). It therefore seems that Peters et al. (2017) included too few sawfly species to reliably recover relationships outside Apocrita, whereas our dataset specifically targeted those relationships through extensive taxon sampling of symphytan lineages. The sister-group relationship of Tenthredinoidea and the remaining Hymenoptera as found by Blaimer et al. (2023) was present in some of our outgroup-rooted phylogenies. However, it is a known issue that outgroup rooting can impact the topology of the ingroup (Gatesy et al., 2007; Holland et al., 2003). Interestingly, we found that including non-hymenopteran outgroups produced different root locations and affected the position of Xyelidae (and thus Xyeloidea). Evidently, the combination of the very long branch connecting Hymenoptera to the outgroups and the short internodes immediately after the crown-group node forms a major challenge for outgroup rooting (Bell et al., 2020). Therefore, we also used RootDigger (Bettisworth and Stamatakis, 2021) to estimate the most probable root position; these analyses recovered Xyelidae as a highly supported, monophyletic sister group to all remaining Hymenoptera. Thus, our results are in line with a series of studies based on morphological (Beutel and Vilhelmsen, 2007; Schulmeister, 2003), molecular (Malm and Nyman, 2015; Tang et al., 2019) and total-evidence analyses (Ronquist et al., 2012; Sharkey et al., 2012).

A big part of the observed topological differences was found between concatenated and coalescent-based species tree methods, and even among the several species tree topologies. This could be caused by the internal and edge trimming of individual UCE alignments during data processing. On one hand, trimming removes poorly aligned sites but, given our broad taxon sampling, it may also remove a lot of the variation and leave very short alignments. This reduction of the phylogenetic signal may result in less accurate estimation of gene trees and, thus, species trees. The difficulty in obtaining informative individual alignments together with potentially variable patterns of molecular evolution even within UCEs (Tagliacollo and Lanfear, 2018) and mutational saturation (Cruaud et al., 2024) can complicate UCE-based species tree reconstruction across deep evolutionary timescales.

For Xyelidae, we estimated a fairly recent crown age, but the long stem leading to the crown group is congruent with the fossil record, which dates the oldest putatively xyelid fossils to the Late Triassic (Grimaldi and Engel, 2005). The Pamphilioidea have occupied various positions in the Hymenoptera tree in previous studies, either as sister to only Unicalcarida (all Hymenoptera except Xyeloidea, Tenthredinoidea

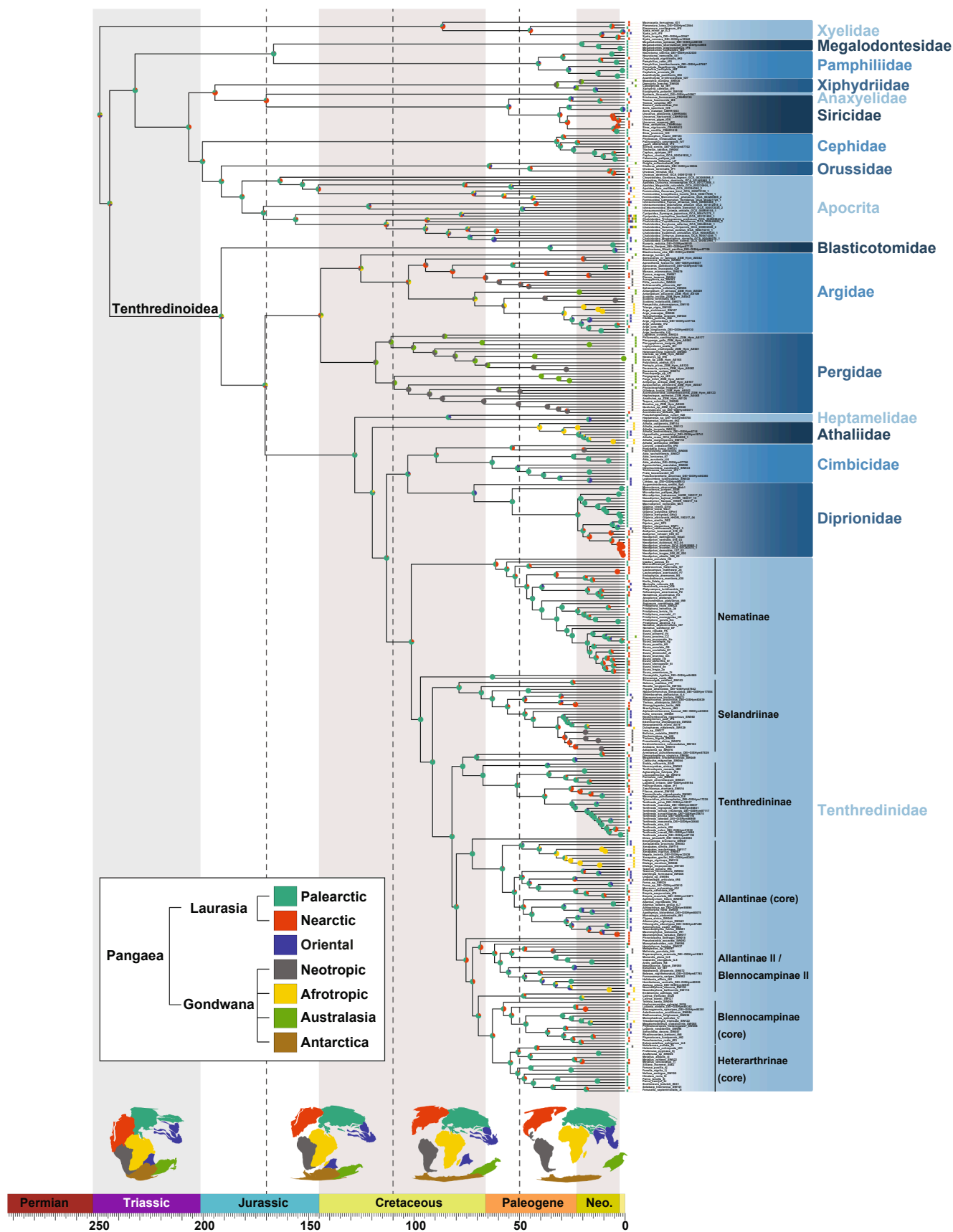


Fig. 4. Ancestral area reconstruction results based on the time-calibrated phylogeny, estimated under the DEC + J model with time constraints (M1 model). Coloured bars next to each terminal taxon show its distribution, pie charts on nodes indicate the relative probabilities of all possible ancestral ranges, and dashed lines separate the time bins used for the M1 model. Maps below the tree illustrate continental configurations within each time bin, and the historical sequence of paleocontinental fragmentation is shown in the legend above the maps.

and Pamphilioidea) (Heraty et al., 2011; Klopstein et al., 2013; Ronquist et al., 2012) or to Tenthredinoidea + Unicalcarida (Malm and Nyman, 2015; Sharkey et al., 2012). Here, we provide further support for the former position as well as for the monophyly of Unicalcarida, which is a widely accepted hymenopteran relationship (Davis et al., 2010; Heraty et al., 2011; Malm and Nyman, 2015; Peters et al., 2017; Sharkey et al., 2012). In general, we observed strong topological consistency among all concatenated RootDigger-rooted trees (Fig. 3). The only exception was the RAxML analysis partitioned by UCE locus, which produced a tree in which Xiphydrioidea was separated from Siricoidea, although with low support. A similar separation of Xiphydrioidea and Siricoidea has been found before (Malm and Nyman, 2015; Ronquist et al., 2012; Sharkey et al., 2012) but the sequence of divergences has differed among studies. This part of the phylogeny among early Unicalcarida appears difficult to resolve, and results seem to be affected by the source of the data, especially when morphological information is included (Klopstein et al., 2013; Ronquist et al., 2012; Sharkey et al., 2012). Nevertheless, most large-scale molecular studies have recovered the same clade formed by Xiphydrioidea and Siricoidea as our most probable topology (Blaimer et al., 2023; Branstetter et al., 2017a; Peters et al., 2017). The relationship of the parasitoid woodwasp family Orussidae as the sister to all Apocrita has been strongly favoured by phylogenomic analyses (Peters et al., 2017; Tang et al., 2019), and is one that is further supported by morphological data, promoting the hypothesis of a single origin of carnivory within the Hymenoptera (Vilhelmsen and Turrissi, 2011).

Tenthredinoidea comprises more than 80 % of described symphytan species and constitutes the most diverse superfamily of the symphytan grade (Taeger et al., 2018). Their ecological and species diversity can be attributed to their ancient association with angiosperms, which Tenthredinoidea colonized soon after the first angiosperms appeared (Nyman et al., 2019). Like in butterflies (Kawahara et al., 2023) and beetles (Mckenna et al., 2015), many tenthredinoid lineages survived the K/Pg mass extinction event, and a rapid radiation coinciding with angiosperm diversification commenced from the Cretaceous onwards. Within Tenthredinoidea, most relationships correspond to earlier analyses. We recovered the monotypic genus *Zenarge* as sister to other Argidae, in line with most prior studies. Malagón-Aldana et al. (2021) recently recovered *Zenarge turneri* as sister to a clade formed by the remaining Argidae and Pergidae, and therefore proposed it to be raised to family status. However, in a subsequent broader re-analysis of Tenthredinoidea with new fossils (Vilhelmsen et al., 2024), *Zenarge* came out as sister to Argidae—the same position as in our and previous studies (Malm and Nyman, 2015), suggesting that erection of a separate family is not needed. The main difference to most prior analyses of Tenthredinoidea is the position of *Athalia* and *Hypsathalia*, which until recently were classified in the tenthredinid subfamily Athaliinae. With their current position outside Tenthredinidae and Cimbicidae + Diprionidae, our results provide strong support for the treatment of Athaliidae as a separate family, suggested by Schulmeister (2003) and Niu et al. (2022). Athaliidae have been placed at various positions within Tenthredinoidea in previous studies (Klopstein et al., 2013; Malm and Nyman, 2015; Niu et al., 2022, 2021; Ronquist et al., 2012). Recently, *Athalia* and related genera were first moved within Tenthredinidae from the subfamily Allantinae to a separate subfamily Athaliinae (Malm and Nyman, 2015) and later promoted further to represent a distinct family (Niu et al., 2022). However, our age estimate for crown Athaliidae (41 Ma) differs greatly from the estimates of Niu et al. (2022) (133 or 143 Ma depending on the markers used). The discrepancy is partly but not entirely explained by the inclusion of the divergent genus *Dentathalia* in the analysis of Niu et al. (2022), because the genus would be placed as sister to the taxa included in our analysis. As our overall analysis includes a wider sample of symphytan lineages and a larger number of fossil calibrations, we tentatively consider our estimate more reliable.

Notably, our inclusion of a large number of taxa from across the

world resulted in para- or polyphyly of several large traditionally defined subfamilies of the largest sawfly family Tenthredinidae. More work therefore seems necessary to fully resolve their phylogenetic status, particularly for Blennocampinae and Allantinae.

4.2. Ancestral range estimation

Large-scale phylogenomic analyses and improved statistical methods are increasingly providing opportunities for inferring deep biogeographic patterns within ancient insect groups (Jiang et al., 2022; Kawahara et al., 2023; Murillo-Ramos et al., 2021). Sawflies assume diverse lifestyles and niches, and collectively utilize a wide variety of host plants (Nyman et al., 2019). As in other insect herbivores (Kawahara et al., 2023; Nylin et al., 2018), different modes of speciation likely have contributed to sawfly evolution and diversification. From a biological point of view, no one biogeographical model can fully reconstruct the entire evolutionary history of sawflies. The three models implemented in BioGeoBEARS differ in the way ranges are inherited along tree branches. The higher support for the DEC and DIVA-like models, among the three considered models with and without the founder-event parameter (+J), indicates that dispersal and vicariance events have been important drivers of sawfly evolution (see also Nyman et al., 2010).

We inferred a Pangaeian distribution as the most likely ancestral area of the hymenopteran MRCA. However, as for other comparably old insect groups (Letsch et al., 2021; Matsumura et al., 2020; Sota et al., 2022), the similar probabilities estimated for each region are likely to reflect uncertainties of the analyses that span a period of 250 million years. Hymenoptera started diversifying during the Late Permian or Early Triassic, prior to the fragmentation of the supercontinent Pangaea. During this time, the warm climate and rapidly diversifying flora (Kustatscher et al., 2018; Preto et al., 2010) likely offered ample ecological opportunities for early plant-feeding Hymenoptera, which then spread all over the supercontinent. However, even during the early phase of the hymenopteran radiation, species-level distributions have probably been geographically restricted, as environmental conditions and vegetation patterns differed across Pangaea (De Baets et al., 2016). Still, the tenthredinoidean ancestors appear to have dispersed globally, a pattern shared with, for example, several clades of Megaloptera (Jiang et al., 2022). In contrast, the ancestors of Xyelidae and other non-tenthredinoid families dispersed primarily in the Northern Hemisphere, possibly due to environmental restrictions, similar to early Plecoptera (Letsch et al., 2021).

Among Pamphilioidea and non-apocritan Unicalcarida, most groups share an ancestral Laurasian origin. Some families in this clade (re-) populated all or parts of Gondwana, such as the ancestors of Orussidae and Xiphydriidae. The worldwide distribution of the Orussidae MRCA can be explained by their carnivorous lifestyle. With larvae feeding on other insects, the ancestor of extant Orussidae and Apocrita discovered a new ecological niche, which resulted in explosive diversification of parasitoid taxa, particularly of wasp-waisted Apocrita (Vilhelmsen and Turrissi, 2011). Today, Orussidae are still distributed globally with highest diversity in tropical regions (Taeger et al., 2018). In a more detailed study of the family, Vilhelmsen (2004) suggested that extant orussids initially radiated in the Southern Hemisphere, but orussid fossils from the Northern Hemisphere (Rasnitsyn and Quicke, 2002; Vilhelmsen et al., 2024) support our inference that early Orussidae were already widespread. However, the sample size included here is too small to draw strong conclusions regarding the biogeographic history of the family. The woodwasp family Xiphydriidae, which contains 146 extant species (Taeger et al., 2018), originated in Gondwana and further diversified through radiations within Australasia and the Neotropics after the breakup of Gondwana. Most of the extant xiphydriid diversity is found in the Northern Hemisphere, which appears to have resulted from a single northward dispersal event ~15 Ma. However, three xiphydriid genera include species that are distributed in the Northern and Southern

Hemisphere (Shinohara, 2022; Taeger et al., 2018), suggesting that more detailed analyses might reveal additional dispersals in the north–south direction. The presence of xiphydriid woodwasps on New Caledonia (Fig. 4; see also (Jennings et al., 2021)), which may have been submerged during the early Cenozoic until ~37 Ma (Kranitz et al., 2014; Pelletier, 2007), indicates considerable capacity for long-distance oceanic dispersal, possibly through rafting as larvae or pupae within floating wood. Unfortunately, there are no xiphydriid fossils available (Gao et al., 2022; Jouault et al., 2022), possibly due to their Gondwanan origin and the comparatively little-studied palaeoentomology of the southern continents. For the Siricidae + Anaxyelidae clade, the estimated Nearctic ancestral range might be a biased result due to the single extant Anaxyelidae species (*Syntexis libocedrii*) having a Nearctic distribution and Siricidae today being found primarily in the Northern Hemisphere (Palearctic, Nearctic, and Southeast Asia). In contrast, both of these families have a rich and ancient fossil record across the globe dating back to the Jurassic (Grimaldi and Engel, 2005), so their current distribution may reflect range contraction driven by extinctions and reductions of gymnosperms in other parts of the world (Crisp and Cook, 2011).

Within Tenthredinoidea, the split between the clade Argidae + Pergidae and the remaining families coincides with the breakup of Pangaea supercontinent (Scotese, 2016; Seton et al., 2012) and may thus reflect a Laurasian–Gondwanan vicariance event. Following the breakup, the families Argidae and Pergidae originated in Gondwana whereas others (Cimbicidae, Diprionidae, Tenthredinidae) were confined to the Northern Hemisphere and, like many non-Tenthredinoidea, independently populated Gondwanan regions. Diversification of Pergidae likely started in Australia and the Neotropics, and bidirectional dispersal of Pergidae via Antarctica continued until Gondwana was fully separated (~50 Ma), agreeing with previous studies (Schmidt and Walter, 2014). For Argidae, the suggested Gondwanan origin is in line with a recent comprehensive study of argid biogeography (Malagón-Aldana et al., 2022). Nevertheless, our results show that the two main clades within Argidae, roughly corresponding to the subfamilies Arginae and Sterictiphorinae, followed different paths. The Arginae ancestor retained a tropical distribution, and representatives of the subfamily later dispersed to the Northern Hemisphere, likely facilitated by the collision of Africa and/or India with the Palearctic. In turn, the MRCA of Sterictiphorinae occupied an ancestral area comprising the Nearctic, Neotropics and Palearctic, whereas extant Sterictiphorinae are distributed mainly in the Neotropics. The ancestral area estimated here might be an artefact caused by our taxon sampling. With higher representation of neotropical lineages, Malagón-Aldana et al. (2022) suggested that both subfamilies have a similar history with an origin in Gondwana and later dispersal to the Northern Hemisphere. For the largest sawfly family, Tenthredinidae, several independent colonizations of the Neotropics, Southeast Asia, or Africa occurred. Similarly, recurrent dispersals between the Palearctic and Nearctic happened within different groups (Siricinae, Diprionidae, Nematinae). All of these groups are associated with northern plant taxa (Siricinae and Diprionidae: conifers, many Nematinae: willows, birches, and conifers). Thus, their frequent and recent interchange across the Bering strait can be attributed to (co)dispersal facilitated by the wide distribution of their respective host-plant taxa across the northern Hemisphere (Seifert et al., 2020; Vila et al., 2011).

Africa is the continent with the second-lowest extant diversity of sawfly species, after Australia (Taeger et al., 2018). Notably, both continents have experienced tectonic northward drift accompanied by substantial aridification during the Cenozoic (Crisp et al., 2004; Jacobs, 2004). The low number of species in these regions could therefore be a result of extinction events during the aridification. For the Australian sawfly fauna this may have been partly compensated by the emergence of plants adapted to the arid environment like *Eucalyptus* (Myrtaceae). About half of the Australian Pergidae and one third of all Australian sawfly species are associated with modern Myrtaceae, whereas a few

smaller subfamilies are still confined in their distribution to patches of rainforest on the continent (Schmidt and Walter, 2014). A similar scenario on the African continent could have driven the evolution of the Afrotropical sawfly fauna, as it has been observed for other insects (bush crickets (Grzywacz et al., 2021), grasshoppers (Hemp et al., 2020)) as well as chameleons (Tolley et al., 2013), whose diversification was closely linked to the aridification and cyclic fragmentation of African rain forests during the Cenozoic. Nowadays, several sawfly clades are primarily distributed in the Afrotropics, such as the argid genera *Pampsilota*, *Triarge*, and African *Arge* species, multiple *Athalia* species, and several tenthredinid genera. However, our results show that the Afrotropical sawfly fauna is a mixture of groups with different biogeographic histories and routes of colonization. Argidae occurred in Africa before it separated from South America ~110 Ma, but the MRCA of the Afrotropical clade evolved in Africa after the separation of Gondwana. *Athalia* similarly evolved and diversified in the Afrotropics. Later, when the African continent collided with the Palearctic in the Early Cenozoic, a secondary dispersal of Athaliidae to the Palearctic occurred. In contrast, according to our results, Tenthredinidae went the other way around, so that several tenthredinid lineages independently dispersed from the Palearctic to Africa after its collision with the Palearctic.

5. Conclusions

By combining dense taxonomic sampling with sequence data from large parts of the genome, we produced the most comprehensive phylogeny of sawflies and woodwasps to date and provided new insights to their deep historical biogeography. Our analyses reveal a highly dynamic pattern of dispersals and re-colonisations which shaped the evolution of Symphyta throughout a period of 250 million years. This study also shows a heterogeneous evolutionary history for the African sawfly fauna. In addition to the biogeographical implications of early hymenopterans presented here, our family-level phylogeny will provide a solid foundation for future studies on diversification dynamics and the role of geography for host-plant co-evolution within specific symphytan groups. Especially, improved interdisciplinary approaches, such as linking climatic and floristic reconstructions as well as fossil data with time-calibrated species distribution analyses, hold the potential to paint an even more detailed and comprehensive picture of Hymenoptera evolution.

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CRediT authorship contribution statement

Saskia Wutke: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stephan M. Blank:** Writing – review & editing, Resources, Data curation. **Jean-Luc Boevé:** Writing – review & editing, Resources, Data curation. **Brant C. Faircloth:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Frank Koch:** Resources. **Catherine R. Linnen:** Writing – review & editing, Resources, Data curation. **Tobias Malm:** Writing – review & editing, Resources, Data curation. **Gengyun Niu:** Writing – review & editing, Resources. **Marko Prous:** Writing – review & editing, Resources, Methodology, Data curation. **Nathan M. Schiff:** Writing – review & editing, Resources, Data curation. **Stefan Schmidt:** Writing – review & editing, Resources, Data curation. **Andreas Taeger:** Writing – review & editing, Resources, Data curation. **Lars Vilhelmsen:** Writing – review & editing, Resources, Data curation. **Niklas Wahlberg:** Writing – review & editing, Resources, Funding acquisition, Data curation. **Meicai Wei:** Resources, Data curation. **Tommi Nyman:** Writing – review &

editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Research data associated with this study are available from NCBI Sequence Read Archive and GenBank, respectively (BioProject accession PRJNA849376) and Zenodo (<https://doi.org/10.5281/zenodo.6651394>) (Wutke et al., 2022).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ympev.2024.108144>.

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