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# Phylogeny of Blattoidea (Dictyoptera: Blattodea) with a revised classification of Blattidae

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## Abstract

Blattoidea are comprised of the major lineages Blattidae, Lamproblattidae, Tryonicidae, Anaplectidae, and Cryptoceridae + Isoptera. Despite a number of studies, no consensus exists regarding the relationships between these lineages. Additionally, the current division of Blattidae into Archiblattinae, Blattinae, Macrocerinae and Polyzosteriinae needs phylogenetic testing. We present a molecular phylogeny of Blattoidea recovering all the major lineages as monophyletic with Lamproblattidae as sister to the remaining Blattoidea and Tryonicidae as sister to Cryptoceridae + Isoptera. Contrary to many previous studies, we found a high degree of consistency between analyses, possibly due to improved taxon sampling. We found that none of the currently accepted subfamilies of Blattidae are monophyletic. Mapping of distribution revealed a clear geographic structuring at odds with the current subfamilial classification. Based on results from this and other studies, we present a revised classification of Blattidae: we erect two new subfamilies, Eurycotiinae **stat. rev.** and Austrostylopyginae **subfam. nov.**, reinstate Duchailiinae **stat. rev.** and subsume Macrocerinae in Polyzosteriinae. We also present a division of Polyzosteriinae into tribes: Polyzosteriini, Methanini **stat. rev.**, Rothsilphini **trib. nov.**, and Celatoblattini **trib. nov.** Within Blattidae, Duchailiinae is sister to the remaining taxa, while Austrostylopyginae is most likely sister to all other Blattidae except Duchailiinae.

## Key words

Archiblattinae, Austrostylopyginae, Blattinae, Duchailiinae, Eurycotiinae, Macrocerinae, Polyzosteriinae, Taxonomy

## 1. Introduction

The systematics of the blattodean superfamily Blattoidea have changed several times within the last decades. Most notably termites, formerly considered an insect order, have been placed within Blattoidea as sister to Cryptoceridae (e.g., Klass 1995; Inward et al. 2007). Other import-

ant changes are the inclusion of Anaplectidae, formerly placed as a subfamily within Blaberoidea (Djernæs et al. 2015), and the elevation of Lamproblattidae and Tryonicidae to family status, both formerly considered subfamilies within Blattidae (Klass and Meier 2006; Murienne

2009). These changes have been based both on morphological (Klass 1995; Klass and Meier 2006), molecular (Inward et al. 2007; Muriene 2009) and combined data (Djernæs et al. 2015).

Recent studies support a monophyletic Blattoidea comprised of the major lineages Blattidae, Lamproblattidae, Tryonicidae, Anaplectidae, and Cryptocercidae + Isoptera (Djernæs et al. 2015, 2020; Wang et al. 2017; Bourguignon et al. 2018; Evangelista et al. 2018), but no consensus exists regarding the relationships between these lineages. For example, Bourguignon et al. (2018) and Evangelista et al. (2018) placed Tryonicidae and Blattidae as sister groups, while Djernæs et al. (2015) and Wang et al. (2017) found evidence for Tryonicidae and Lamproblattidae as sister groups. Within Blattoidea, Djernæs et al. (2015) and Evangelista et al. (2018) found the position of Lamproblattidae and Anaplectidae to be highly labile.

The clade Cryptocercidae + Isoptera is the most speciose lineage within Blattoidea with nearly 3000 species, the vast majority belonging to Isoptera (Beccaloni and Eggleton 2013). This group has been the subject of several recent phylogenetic studies (e.g. Cameron et al. 2012; Bourguignon et al. 2014; Wu et al. 2018; Bucek et al. 2019). By contrast, Blattidae, with c. 650 species (Beccaloni 2014), has not been the main subject of any recent phylogenetic study.

Furthermore, the current division of Blattidae into the subfamilies Archiblattinae, Blattinae, Macrocercinae and Polyzosteriinae might not reflect evolutionary history. For example, the nominally polyzosteriine genus *Eurycotis* has been placed as sister to Archiblattinae + Blattinae by Djernæs et al. (2015) and Liao et al. (2021), or, together with *Pelmatosilpha*, as sister to Archiblattinae + Blattinae + Polyzosteriinae (Legendre et al. 2015; Evangelista et al. 2018). However, Bourguignon et al. (2018) placed *Eurycotis* as sister to the remaining Polyzosteriinae. Several phylogenetic studies have placed (parts of) Archiblattinae within Blattinae (Djernæs et al. 2015; Wang et al. 2017; Bourguignon et al. 2018; Evangelista et al. 2018; Liao et al. 2021), while other studies have placed Archiblattinae as sister to Blattinae (Inward et al. 2007; Legendre et al. 2015; Evangelista et al. 2019). Phylogenetic studies have consistently placed *Duchailuia* as sister to all other Blattidae (Djernæs et al. 2015; Wang et al. 2017; Evangelista et al. 2019), and Roth (2003a) placed *Duchailuia* in a separate subfamily. However, Anisyutkin and Telnov (2018) placed the genus within Blattinae. Finally, representatives of Macrocercinae have never previously been included in a phylogenetic study.

Djernæs et al. (2020) found a high degree of congruence between geographic distribution and phylogeny within Blaberidae, and, like Svenson and Whiting (2009) for Mantodea and Simon et al. (2019) for Phasmatodea, found that geographic distribution is more congruent with phylogeny than the traditional classification is.

Our aim was to produce a molecular phylogeny illuminating the relationships between the major blattoidean lineages (Blattidae, Lamproblattidae, Tryonicidae, Ana-

plectidae, and Cryptocercidae + Isoptera) and to clarify the monophyly of the blattid subfamilies as well as the relationships between them. To accomplish this, we sampled several representatives for all major blattoidean lineages and, within Blattidae, representatives for all currently recognised blattid subfamilies as well as *Duchailuia*. Our taxon sampling covers the majority of blattid genera, generally with multiple representatives of each genus. We used data from nine genes, both mitochondrial and nuclear, for our phylogenetic analyses. We mapped geographic distribution and discuss the results. Based on our results and results from other studies, we propose a revised classification of Blattidae.

## 2. Material and methods

### 2.1. Taxon sampling

The study includes 131 ingroup taxa (Blattoidea), 19 near outgroup taxa (other Dictyoptera), and 9 far outgroup taxa (other Polyneoptera + Odonata), for a total of 159 taxa. The ingroup includes multiple representatives for all major blattoidean lineages (Blattidae, Lamproblattidae, Tryonicidae, Anaplectidae, and Cryptocercidae + Isoptera). The ingroup also includes multiple representatives for all currently recognised blattid subfamilies (Archiblattinae, Blattinae, Macrocercinae, and Polyzosteriinae) and a representative of the genus *Duchailuia* (Blattinae). Several putatively conspecific, but genetically distinct, individuals are included in the data set (see Table S1). This is the case for e.g. *Lamproblatta albipalpus* Hebard, for which two specimens, *L. albipalpus* MD-2014 and *L. albipalpus* TB-2018 exhibit at least 8% sequence divergence in all overlapping sequences; percent sequence divergence based on BLAST results from GenBank ([www.ncbi.nlm.nih.gov/genbank](http://www.ncbi.nlm.nih.gov/genbank)). In general, sequences from different specimens were not combined as a single terminal taxon if the sequence divergence exceeded 3% in any overlapping sequences. The only exception to this rule was *Eurycotis floridana* (Walker) in which the complete mitochondrial sequence (GenBank # MG882177) was very similar to sequences from other included conspecifics based on 12S and COI+II (< 1% divergence), but highly divergent based on 16S (> 7% divergence). The 16S sequence used for *E. floridana* (GenBank # KP986295) is very similar (< 1% divergence) to the third available *E. floridana* 16S sequence (GenBank # JN615296). Named species were combined with congeneric 'sp.'s or 'cf.'s if the sequence divergence of all overlapping sequences was less than 1%. These cases are indicated in Table S1 as e.g. *Shelfordella lateralis* (Walker)/sp. MNHN BL113, but otherwise just referred to by the species name, here *S. lateralis*. We generally follow the taxonomy of Cockroach Species File (Beccaloni 2014), but within Blaberoidea we follow Djernæs et al. (2020) and Evangelista et al. (2020).

## 2.2. Data and alignment

The data set consists of sequences from 9 genes that are widely used for resolving cockroach relationships (e.g. Inward et al. 2007; Djernæs et al. 2012, 2015, 2020; Legendre et al. 2015, 2017; Wang et al. 2017). Six mitochondrial genes: the ribosomal genes 12S (c. 375 nucleotides [nt] fragment) and 16S (c. 415 nt), the protein coding genes COI (c. 1490 nt fragment, but many sequences only a 658 nt fragment) and COII (c. 690 nt), and the tRNA genes tRNA-leu (c. 75 nt) and tRNA-lys (c. 40 nt fragment). Three nuclear genes: the ribosomal genes 18S (c. 1825 nt) and 28S (c. 520 nt fragment), and the protein coding gene H3 (c. 330 nt fragment). The total length of the aligned data set is 7147 nt. Our data set provides sequence data for 37 species of Blattidae and a species of Tryonicidae not previously sampled, as well as adding newly sequenced gene coverage to previously sampled species. Sequencing was done using standard methods: Samples contributed by JM (see Table S1) were extracted using the DNeasy Tissue Kit (Qiagen, Valencia, CA) and amplified using Ready-ToGo polymerase chain reaction Beads (GE Healthcare, Piscataway, NJ). The mitochondrial 12S and 16S fragments were amplified using the 12Sai/12Sbi and 16SA/16SB primers respectively (Kambhampati 1995). The barcode fragment of the mitochondrial COI was amplified using the LCO1490/HCO2198 primers (Folmer et al. 1994). The nuclear 18S was amplified using the primer pairs 18S1F/18S5R, 18S3F/18Sbi and 18SA2.0/18S9R (Giribet et al. 1996; Whiting et al. 1997). The nuclear 28S was amplified using the 28Sa/28Sbout primers (Nunn et al. 1996). The nuclear H3 was amplified using the H3aF/H3aR primers (Svensson and Whiting 2004). The PCR protocol was 94°C for 5 min, followed by 35 cycles of 94°C (15 s), 50°C (15 s) and 72°C (15 s), and then a final extension of 72°C (7 min) on MJ Research Peltier Thermal Cyclers (MJ Research Inc., Waltham, MA). Each 25 µL reaction contained 1 µL of each 10 mm primer, 2 µL of template and 21 µL of water. PCR products were purified using AMPure magnetic bead purification (Agencourt Bioscience Corp., Beverly, MA) on a Biomek NX robot (Beckman Coulter, Fullerton, CA). Amplification products were then sequenced in both directions. Each reaction mixture contained 1 µL BigDye (Applied Biosystems), 1 µL of 3.2 mm primer, 1 µL BigDye Extender Buffer (Applied Biosystems) and 5 µL of DNA template. Sequencing reactions ran for 25 cycles of 96°C (15 s), 50°C (15 s) and 60°C (4 min). Sequences were purified using CleanSeq magnetic bead purification (Agencourt Bioscience Corporation) on a Biomek NX robot (Beckman Coulter) to remove unincorporated primers and dyes. Products were re-suspended in 40 µL of 0.5 mM EDTA and were electrophoresed in an ABI Prism 3730xl sequencer (Applied Biosystems). Samples contributed by MD (see Table S1) were produced following Djernæs et al. (2015). All new sequences were checked for contamination using unrestricted BLAST searches on GenBank. The new sequences were combined with sequences from GenBank and

BOLD (<http://www.boldsystems.org>) to produce the data set.

The sequences were aligned in MAFFT 7.471 (Katoh et al. 2005, 2019; Katoh and Standley 2013) using the G-INS-1 algorithm. Distance trees (Neighbour Joining) were produced for each alignment in MAFFT to check for incorrectly identified GenBank or BOLD sequences. All alignments were checked visually and manual corrections were made in Mesquite v. 3.03 (build 702; Maddison and Maddison 2015).

Our taxon sampling approach resulted in a data set with missing data that could lead to lack of resolution and/or low support values. To alleviate this potential issue, we ran analyses both on the complete data set and on a reduced (trimmed) data set. To produce the trimmed data set, we excluded taxa that did not have coverage for at least three of the genes 12S, 16S, COI, COII, 18S, 28S or H3 (tRNA-leu and tRNA-lys not considered due to their short length). This resulted in the exclusion of 22 taxa from the trimmed data set: *Catara rugosicollis* (Brunner von Wattenwyl), *Cartoblatta scorteccii* Princis 471A, *C. scorteccii* 474A, *Celatoblatta vulgaris* (Johns), *Hebardina concinna* (Haan), *Maoriblatta novaseelandia* (Brunner von Wattenwyl), *Pseudoderopeltis bimaculata* (Walker), *Macrocerca* sp. 1 FL-2016, *Anamesia maculosa* Mackerras, *Anamesia lambii* Tepper, *Desmozosteria scripta* Mackerras, *Desmozosteria cincta* Shelford, *Eppertia furcate* (Tepper), *Eppertia* sp. ANIC, *Eurycotis bahamensis* Rehn, *Euzosteria nobilis* (Brunner von Wattenwyl), *Euzosteria sordida* Shaw, *Megazosteria patula* (Walker) 000186, *Pallidionicus pandanorum* Grandcolas, *Polyzosteria limbata* Burmeister, *Zonioploca pallida* Shelford, and *Zonioploca* sp. This exclusion did not affect our taxonomic coverage at the family or subfamily level, only at the genus and species level.

## 2.3. Partitioning and phylogenetic analyses

We partitioned the data according to origin (mitochondrial vs. nuclear) and gene type (protein coding vs. rRNA and tRNA), resulting in four partitions: **1)** mitochondrial rRNAs and tRNAs (12S, 16S, tRNA-leu and tRNA-lys), **2)** mitochondrial protein coding genes (COI and COII), **3)** nuclear rRNAs (18S and 28S), and **4)** nuclear protein coding gene (H3). We then added further partitioning by gene type (rRNA vs tRNA), and partitioning by level of variation (variable vs conserved regions of 18S and 28S; 12S and 16S in the present data set did not have the long conserved regions characteristic of 18S and 28S). Variable versus conserved regions was determined by visual evaluation of the alignment in Mesquite. This further partitioning resulted in six partitions: **1)** mitochondrial rRNAs (12S and 16S), **2)** mitochondrial protein coding genes (COI and COII), **3)** mitochondrial tRNAs (tRNA-leu and tRNA-lys), **4)** nuclear rRNAs, variable regions (variable regions of 18S and 28S), **5)** nuclear rRNAs, conserved regions (conserved regions of 18S and 28S), and **6)** nuclear

protein coding gene (H3). We then added partitioning by gene, resulting in ten partitions: **1)** 12S, **2)** 16S, **3)** COI, **4)** COI, **5)** tRNA-leu and tRNA-lys, **6)** variable regions of 18S, **7)** conserved regions of 18S, **8)** variable regions of 28S, **9)** conserved regions of 28S, and **10)** H3. We tested additional partitioning by codon position (resulting in 16 partitions), but this led to a lack of convergence in the Bayesian Inference analyses and clear artefacts in the resulting trees (e.g. taxa included based on just the COI barcode fragment forming a clade apart from closely related taxa with more complete data), problems likely caused by over-parameterization (Ronquist et al. 2020).

We analysed both the complete and trimmed data sets using the three above-mentioned partitioning schemes (4, 6 and 10 partitions) allowing us to explore the effect of different partitioning schemes which can affect tree topology (Kainer and Lanfear 2015). Bayesian Inference (BI) analyses were performed in MrBayes 3.2.7a (Ronquist et al. 2012) on Cipres XCEDE (Miller et al. 2010) using model jumping with a gamma model for variation across sites. Model jumping allows MrBayes to sample across the entire GTR model space, a more elegant alternative to *a priori* model testing (Ronquist et al. 2020). The Temp parameter was set to 0.05, changed from the default of 0.1 to facilitate swapping between chains. Analyses of the trimmed data set were run for 10 million generations, sampled every 1000 generations, with burninfrac set to 0.5 and burnin set to 5000 trees. Analyses of the complete data set were run for 50 million generations, sampled every 10000 generations, with burninfrac set to 0.5 and burnin set to 2500 trees. Convergence was evaluated by a visual inspection of the log likelihood plot and by the average standard deviation of split frequencies being < 0.01. Maximum Likelihood (ML) analyses were performed in Garli 2.01 (Zwickl 2006) on Cipres XCEDE. For each partition we used the GTR submodel with the highest posterior probability from the corresponding BI analysis. Models and the overall rate were unlinked across partitions. *Enallagma cyathigerum* (Charpentier) was specified as outgroup to facilitate production of consensus trees. The ML analyses were terminated after 20,000 generations without significant change of topology. Ten independent runs of each ML analysis were performed and the best trees were chosen based on likelihood values (T-ML-4: 3 trees; T-ML-6: 9 trees; T-ML-10: 9 trees; C-ML-4: 3 trees; C-ML-6: 8 trees; C-ML-10: 2 trees). From these, a majority rule consensus tree was produced in Mesquite. Bootstrap analyses were run with 1000 bootstrap repetitions and one tree search repetition per bootstrap repetition, settings otherwise as above. Bootstrap values were calculated in Mesquite.

We chose to use Garli rather than e.g. IQ-TREE or RAxML as the latter programs were developed to analyse phylogenomic data with thousands of taxa and hundreds of thousands to millions of nucleotides (Stamakis 2008; Minh et al. 2021). Our complete data set contains 159 taxa and 7147 nucleotides, and is thus not the type or size of data set that IQ-TREE and RAxML were developed for.

## 2.4. Geographical distribution

Data on geographical distribution are mainly from Princis' catalogue (Princis 1965a, 1966, 1971). Distribution data for species described after 1970 are from the original descriptions. Data from Princis (1965a, 1966, 1971) and original descriptions were supplemented with field collecting data when available. Data for various unnamed species (sp.) are from GenBank, from Bourguignon et al. (2018: table S1), and collecting data (new specimens). When several conspecifics are included as terminal taxa (e.g. three nominal *Tryonicus parvus* (Tepper); see criteria for inclusion in section 2.1.), the distribution data are based on specimen data, not data for the nominal species. The exception is *Cartoblatta scortecii*, in which both included specimens were intercepted at port facilities; in this case the data from Princis (1966) were used. We scored distribution of widespread pest species as inapplicable.

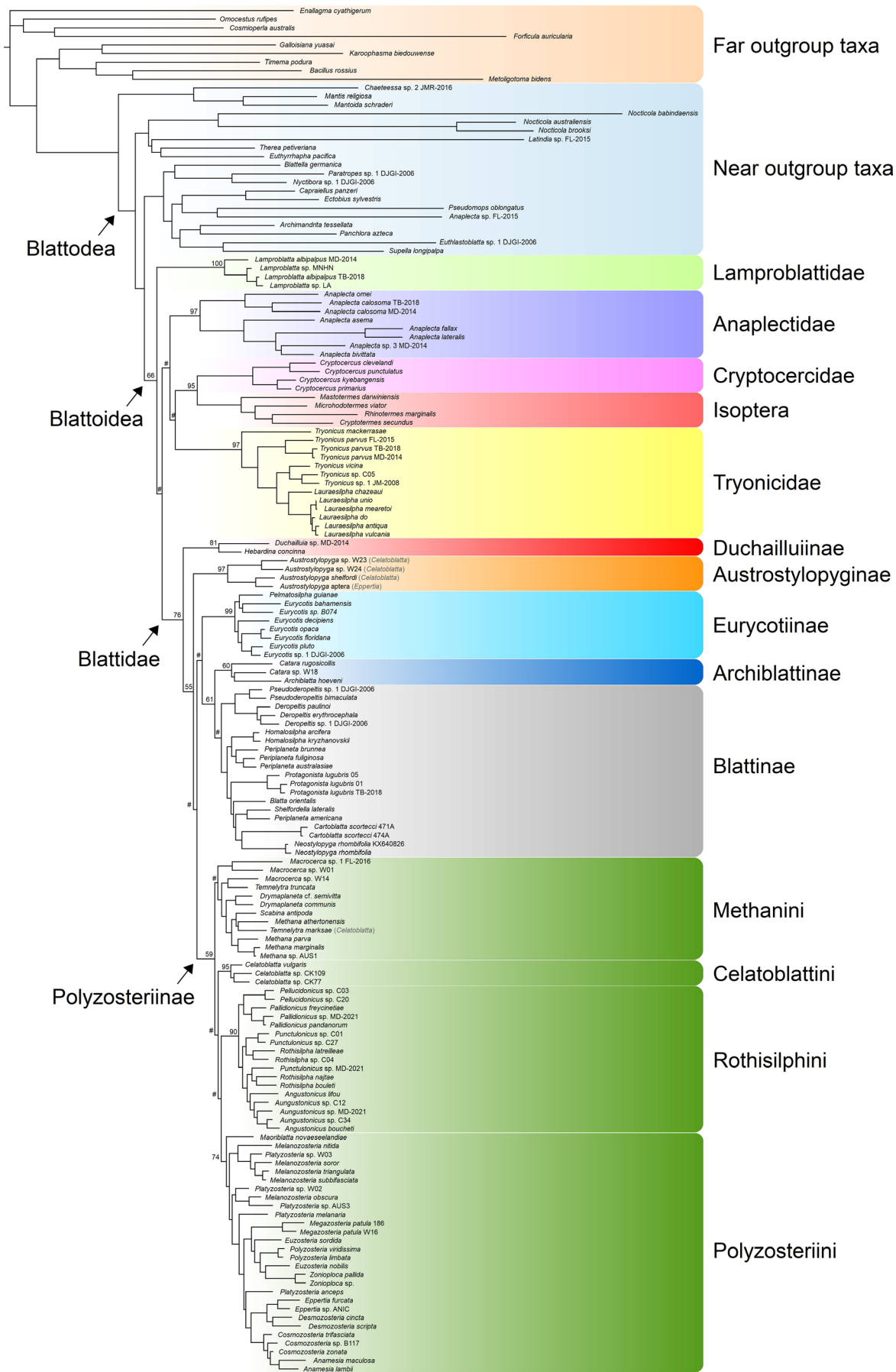
We followed the definitions of biogeographic realms of Olson et al. (2001), with the modifications used by Djernæs et al. (2020). Thus, we included all of Mexico in the Neotropics, included Oceania in Australasia, divided the Palearctic into East and West (along the Ural Mountains) and included all of China (unless more specific locality information was available) in East Palearctic. Additionally, as more than half of the included Blattoidea are from Australasia, we used a finer scale of geographic distribution within this region. This resulted in 10 biogeographic areas: 1) Nearctic, 2) Neotropics, 3) Afrotropics, 4) East Palearctic, 5) Indo-Malaya, 6) Australia, 7) New Guinea, 8) New Caledonia, 9) New Zealand, and 10) remaining Australasia, the latter five subregions of Australasia (no Blattoidea from West Palearctic included).

We mapped geographic distribution in Mesquite on our preferred tree, the tree resulting from the Maximum Likelihood analyses of the complete data set with 6 partitions (C-ML-6). We used parsimony reconstruction of ancestral states and treated the characters as unordered. When a terminal taxon occurred in more than one biogeographical area, we scored it as present in all relevant areas.

## 3. Results

### 3.1. Phylogenetic analyses

The phylogenetic analyses generally gave consistent results with all analyses finding the same relationships between the major lineages of Blattoidea (Blattidae, Lamproblattidae, Tryonicidae, Anaplectidae, and Cryptocercidae + Isoptera). Lamproblattidae was sister to the remaining Blattoidea and Tryonicidae was sister to Cryptocercidae + Isoptera (Fig. 1). All the major blattoidean lineages were monophyletic, except Anaplectidae: *Anaplecta* sp. FL-2015 was consistently placed outside Blattoidea as sister to *Pseudomops oblongatus* (Linnaeus



**Figure 1.** Tree from Maximum Likelihood analysis of the complete data set using 6 partitions (C-ML-6). Subfamily, tribe and genus names and assignments reflect the taxonomic changes made in the present paper; ‘old’ genus names are given in parentheses (in grey). Bootstrap support values for clades of interest are shown, # indicate a bootstrap support < 50. Trees from other analyses essentially agree with this tree, with some minor differences within Blattidae (see Table S2).

us) (Blattellidae). See Table S2 and Figures S1–S12 for support values. Within Blattidae, none of the currently accepted subfamilies were monophyletic and some relationships between clades differed between analyses, although most analyses found the same relationships between clades as depicted in Fig. 1. Differences from this pattern were found in some analyses of the complete data set, see Table S2. We chose the tree from the Maximum Likelihood analysis of the complete data set (C-ML-6) as our ‘preferred tree’. This tree has the same relationships between clades as found in the majority of analyses, and it was based on the complete data set, thus showing the phylogenetic position of all the included taxa.

The trees based on the trimmed data set generally had higher support values, both posterior probabilities and bootstrap values (Table S2). In the Bayesian analyses, the trees based on the trimmed data set were more resolved, while all Maximum Likelihood trees (majority rule consensus trees) were completely resolved. Bayesian analyses of the trimmed data set reached convergence (average standard deviation of split frequencies < 0.01) much faster than analyses of the complete data set (trimmed data set 1.8–8.7 million generations, 6–25 h; complete data set 30.3–42.3 million generations, 110–125 h).

### 3.2. Distribution mapping

Distribution mapping reveals clear geographic structuring with many clades restricted to one or two (neighbouring) geographic areas (Fig. 2). In general, the geographic structuring is clearer in the more densely sampled parts of the tree (compare e.g. Isoptera and Blattidae). Within Blattidae, the majority of Blattinae and Archiblattinae occurs in the Afrotropics and Indo-Malaya, while the majority of Polyzosteriinae is restricted to Australasia. Within Polyzosteriinae, several geographically restricted clades occur (restricted to Australia + New Guinea, to New Caledonia and to New Zealand). It is especially worth noting the clear geographic structuring in Blattidae compared to the lack of monophyly of the currently accepted subfamilies.

## 4. Discussion

Blattoidea as well as the constituent major lineages (Blattidae, Lamproblattidae, Tryonicidae, Anaplectidae, and Cryptocercidae + Isoptera) were monophyletic in all analyses with the exception of *Anaplecta* sp. FL-2015, which was placed within Blaberoidea. However, the placement of this individual is consistent with Legendre et al. (2015) and Evangelista et al. (2018), and the specimen might belong to Pseudophyllodromiidae (see placement in Evangelista et al. 2018: app. D). The assignment of this specimen to *Anaplecta* is either a case of misidentification or the genus *Anaplecta* being poorly defined (Evangelista et al. 2018). With the exclusion of *Anaplecta* sp. FL-2015,

Blattoidea and the constituent major lineages were supported by high posterior probabilities (pp 98–100) and reasonable to high bootstrap values (bs 66–100).

### 4.1. Relationships between major lineages

The relationships between the major lineages of Blattoidea were consistent between all analyses, generally with a pp > 90, but with bs < 50 in all cases (see Table S2). We found Lamproblattidae as sister to the remaining Blattoidea (pp 100, bs 66–82), and Tryonicidae as sister to Cryptocercidae + Isoptera (pp 75–95, bs < 50). Anaplectidae was sister to Tryonicidae + Cryptocercidae + Isoptera (pp 94–98, bs < 50), and this clade was in turn sister to Blattidae (pp 92–97, bs < 50). This agrees partially with Djernæs et al. (2015: fig. 3), but not with Wang et al. (2017), Bourguignon et al. (2018), Evangelista et al. (2018, 2019), Bläser et al. (2020) or Djernæs et al. (2020). Wang et al. (2017) found Anaplectidae as sister to Cryptocercidae + Isoptera and placed Tryonicidae and Lamproblattidae as sister groups. Bourguignon et al. (2018) found Blattidae + Tryonicidae as sister to Cryptocercidae + Isoptera and placed Anaplectidae and Lamproblattidae as sister groups. Evangelista et al. (2018, 2019) and Bläser et al. (2020) found Lamproblattidae as sister to Cryptocercidae + Isoptera and placed Blattidae and Tryonicidae as sister groups. Thus, no consensus exists regarding the relationships between the major blattoidean lineages. Furthermore, both Djernæs et al. (2015) and Evangelista et al. (2018) reported lack of consistency between analyses; the positions of Lamproblattidae and Anaplectidae respectively were very labile. Wang et al. (2017: fig. 1) also found that the relationships between the major lineages differed between analyses. Compared to these previous studies, our study presents an improved taxon sampling, especially for Lamproblattidae and Tryonicidae, which may be responsible for the increased consistency between analyses run under different conditions.

Morphological phylogenetic analyses of these taxa did not recover Blattoidea (Klass and Meier 2006; Djernæs et al. 2015: fig. S13), and so are of limited use regarding the reconstruction of relationships between the major lineages.

Thus, neither molecular nor morphological data offer any firm conclusions regarding these relationships. However, if the internal consistency between analyses in this study is due to increased taxon sampling, increasing the taxon sampling could lead to better consistency between studies. In Blattidae, multiple representatives from all subfamilies should be included if possible (see section 4.6. for revised classification of Blattidae). Additionally, an increased taxon sampling of Anaplectidae, Lamproblattidae and Tryonicidae is desirable, see sections 4.2., 4.3., and 4.4. for details. The taxon sampling of Cryptocercidae + Isoptera is good across most studies, leaving limited room for improvement, although gene coverage for *Cryptocercus clevelandi* Byers could be improved.

## 4.2. Anaplectidae

Anaplectidae (excl. *Anaplecta* sp. FL-2015, see above) was divided into two groups, a Neotropical group and a group found in East Palearctic (China) and Australasia (Australia) with high support (pp 99–100, bs 99–100). Within the latter group, the two Australian specimens form a clade; both are identified as *Anaplecta calosoma* Shelford, but show > 17% divergence in the mitochondrial DNA, so are unlikely to belong to the same species. For comparison, a recent study of ten Chinese *Anaplecta* species found the largest interspecific difference in COI to be 16.8% (Deng et al. 2020). Furthermore, the type locality of *A. calosoma* is New Guinea (Shelford 1912), so it is possible that neither of the Australian specimens identified as *A. calosoma* actually belong to the species described by Shelford.

As currently defined, the family Anaplectidae contains two genera [*Anaplecta* (102 species) and *Maraca* (one species)] and occurs across five biogeographic regions [Neotropic, Afrotropic, East Palearctic, Indo-Malaya and Australasia (Beccaloni 2014; Deng et al. 2020)]. *Anaplecta* species from the Neotropics, East Palearctic, Indo-Malaya and Australasia have been included as terminal taxa in this and other phylogenetic studies (several Chinese species, including *A. omei* Bey-Bienko, occurs both in the East Palearctic and in Indo-Malaya, Deng et al. 2020). African *Anaplecta* have never been included in modern phylogenetic studies (unless *Anaplecta* sp. FL-2015 is a representative of the African Anaplectidae; no locality information was available from GenBank or the original manuscript). McKittrick (1964) studied three species of *Anaplecta*, two Neotropical and one African, and noted that they form a very distinct group, despite differences in the female genitalia indicating that they should not all belong to the same genus. Thus, the genus *Anaplecta* as currently defined is likely a coherent unit, but might need to be split into two or more genera as it consists of a number of morphologically and genetically distinct groups (McKittrick 1964; Djernæs 2015; Wang et al. 2017; this paper).

Future phylogenetic studies of Anaplectidae should include the Neotropical *Maraca fossata* Hebard to confirm whether it belongs in Anaplectidae, and if so, if it should be a separate genus or belongs among the Neotropical members of *Anaplecta*. The latter might be quite likely as Hebard (1926) considered *M. fossata* particularly close to specific Neotropical *Anaplecta* species, although the antenna and pronotum are different.

Apart from the question of the correct placement of *M. fossata*, some subdivision of the many species placed in *Anaplecta* would be appropriate as also suggested by McKittrick (1964). The geographical divisions within *Anaplecta* found in this study are consistent with results of other studies (Djernæs et al. 2015, 2020; Wang et al. 2017; Evangelista et al. 2018). If a denser sampling of *Anaplecta* with better geographic coverage confirms well-supported geographical groups, this might form the basis for a division of *Anaplecta* into several genera. For this, an increased sampling of Australian and Asian taxa

is desirable, but inclusion of African Anaplectidae could be even more important as these have never been included in phylogenetic studies.

## 4.3. Lamproblattidae

As currently defined, the family Lamproblattidae contains three Neotropical genera, *Lamproblatta*, *Lamproglanidifera* and *Eurycanthablatta* (Beccaloni 2014). So far, only *Lamproblatta* species have been included in phylogenetic studies, the genus often represented by a single specimen (e.g. Djernæs et al. 2012, 2015, 2020; Legendre et al. 2015; Wang et al. 2017; Evangelista et al. 2018, 2019), although Bourguignon et al. (2018) included two specimens. We included four representatives of *Lamproblatta*, and found that the deepest split was between a Costa Rican *Lamproblatta*, nominally *L. albipalpus*, and the three *Lamproblatta* specimens from French Guiana, one of which is also nominally *L. albipalpus*. The two specimens identified as *L. albipalpus* show > 8% divergence in the mitochondrial DNA (12S 9%, 16S 11%, COI+II 12%), so are unlikely to belong to the same species. Furthermore, both specimens originate in localities rather distant from the type locality in Colombia (Hebard 1919); *Lamproblatta* is flightless, so is not expected to be highly mobile. Thus, neither of the two nominal *L. albipalpus* specimens might actually be *L. albipalpus*, underlining the need for a revision of this genus, which was last done by Rehn (1930).

The inclusion of *Lamproglanidifera* and *Eurycanthablatta* in future studies is desirable both to test their placement in Lamproblattidae, and to improve the taxon sampling of this family. The inclusion of *Eurycanthablatta* is especially important as Fritzsche et al. (2008) noted similarities in the male genitalia to both *Lamproblatta* and *Cryptocercus*; thus, *Eurycanthablatta* might be a key taxon when trying to find the sister group of *Cryptocercus* + Isoptera.

## 4.4. Tryonicidae

The family Tryonicidae as currently defined contains two genera, *Tryonicus* and *Lauraesilpha*, occurring in Australia and New Caledonia (Beccaloni 2014), with the two genera considered sister taxa (Murienne et al. 2008; Legendre and Grandcolas 2018), a placement supported by Murienne et al.'s (2008) and Murienne's (2009) phylogenetic analyses. However, results from Djernæs et al. (2015, 2020) and Wang et al. (2017) suggests that *Tryonicus* is paraphyletic with respect to *Lauraesilpha*. The increased sampling of *Tryonicus* in this study (seven terminal taxa compared to at most two in any previous studies) allowed us to investigate the possible paraphyly of *Tryonicus* more thoroughly. Our results place *Lauraesilpha* deep within *Tryonicus*, consistent with Djernæs et al. (2015, 2020) and Wang et al. (2017), but as sister to the New Caledonian species of *Tryonicus*, consistent with Murienne et al. (2008) and Murienne (2009).



Our sampling of *Tryonicus* includes *T. mackerrasae* Roth (Australia), three specimens of *T. parvus* (Australia), *T. vicina* (Chopard) (New Caledonia), and two New Caledonian *Tryonicus* sp. Within *T. parvus*, specimen FL-2015 shows 9–13% difference in mitochondrial DNA to MD-2014 and TB-2018, although the three specimens do form a highly supported clade (pp 100, bs 100).

These results highlight the need for a revision of Tryonicidae. Roth (1987) revised *Tryonicus* (including *Lauraesilpha angusta* (Chopard), which was then *Tryonicus angusta*) and considered *Tryonicus monteithi* Roth, *T. mackerrasae* and a possible third species more closely related to each other than to *T. parvus* or *L. angusta*. Our results suggest that either *Lauraesilpha* should be subsumed in *Tryonicus*, or *Tryonicus* should be split into at least three genera: one containing *T. mackerrasae* (and likely *T. monteithi*, Roth 1987), one containing *T. parvus* sensu lato, and one containing the New Caledonian *Tryonicus* species. As *Lauraesilpha* forms a well-supported monophyletic group (Muriene et al. 2008; Muriene 2009; this study) with a distinctive mode of life (xylophagous, tunnelling in rotten branches) compared to other Tryonicidae which live under stones or pieces of dead wood (Roth 1987; Grandcolas 1997), we favour splitting *Tryonicus* rather than subsuming *Lauraesilpha*. However, as there seems to be several undescribed species of *Tryonicus* both in Australia (Roth 1987; this study) and in New Caledonia (Muriene pers. obs.), any taxonomic changes should await a better taxon sampling and description of new species. With regard to the exact placement of Tryonicidae within Blattodea, an increased sampling of Australian Tryonicidae might be beneficial, due to the subordinate position of the New Caledonian taxa.

#### 4.5. Cryptocercidae + Isoptera

Cryptocercidae + Isoptera formed a highly supported monophyletic group in all analyses (pp 100, bs 94–100), consistent with previous studies (e.g. Inward et al. 2007; Djernæs et al. 2015; Legendre et al. 2015; Wang et al. 2017; Bourguignon et al. 2018; Evangelista et al. 2018, 2019). The relationship between the included *Cryptocercus* species is consistent with that found by Che et al. (2016, 2020) and the relationship between the included Isoptera species is consistent with the results of e.g. Cameron et al. (2012), Bourguignon et al. (2014), Wu et al. (2018), and Bucek et al. (2019). However, the taxon sampling in our study does not provide any new information about the relationships within Cryptocercidae or Isoptera compared to these studies, which focused explicitly on these relationships (for Cryptocercidae, see also e.g. Lo et al. 2006; Bai et al. 2018).

#### 4.6. Blattidae

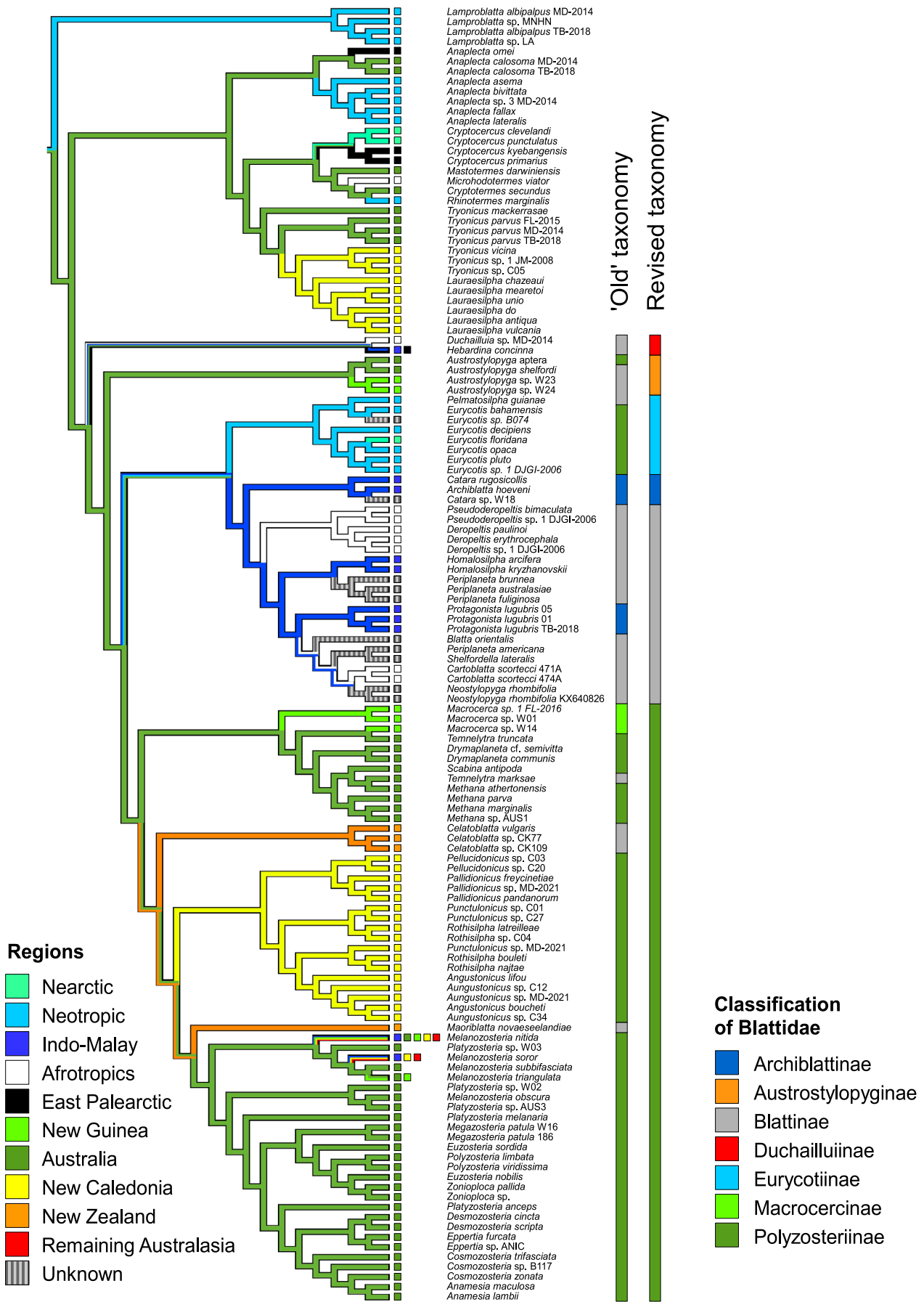
Blattidae was monophyletic in all analyses, but none of the subfamilies as currently defined (Archiblattinae, Blattinae, Macrocerinae and Polyzosteriinae) were mono-

phyletic. Additionally, several genera could not be placed in any of these subfamilies, emphasizing the need for a revised classification of Blattidae. The non-monophyly of the blattid subfamilies is generally consistent with other studies with a sizeable sampling of blattids (Macrocerinae have not previously been included in any phylogenetic studies). Legendre et al. (2015) and Evangelista et al. (2018) found both Blattinae and Polyzosteriinae to be non-monophyletic (only a single representative of Archiblattinae included in both studies). Bourguignon et al. (2018) found Blattinae, but not Polyzosteriinae to be non-monophyletic (only a single representative of Archiblattinae included) while Wang et al. (2017) and Liao et al. (2021) found Blattinae, Polyzosteriinae, and Archiblattinae to be non-monophyletic. Distribution mapping showed a clear geographic structuring within Blattidae (Fig. 2), and a greater congruence between phylogeny and distribution than between phylogeny and current classification, similar to the patterns found by e.g. Svensson and Whiting (2009, Mantodea), Simon et al. (2019, Phasmatodea) and Djernæs et al. (2020, within Blaberidae). Based on the results from this and other studies, we present and discuss a revised classification of Blattidae. The revised placement of all blattid genera included or discussed in this study is shown in Table 1 with the relevant references.

##### 4.6.1. Blattinae

Blattinae as currently defined (henceforth called Blattinae s.l.) was non-monophyletic in all our analyses, with the genera *Celatoblatta*, *Duchailuia*, *Hebardina*, *Maoriblatta* and *Pelmatosilpha* being placed outside the clade containing the type genus *Blatta* and the majority of the included blattine genera (henceforth called Blattinae s.s.). Thus, the geographic distribution of Blattinae s.s. is generally restricted to the Afrotropics and Indo-Malaya (Fig. 2). Additionally, *Protagonista* (currently placed in Archiblattinae) was nested deep within Blattinae s.s. This is generally consistent with other studies that have included any of these genera (Djernæs et al. 2015, 2020; Legendre et al. 2015; Wang et al. 2017; Bourguignon et al. 2018; Evangelista et al. 2018). Although Blattinae s.l. was non-monophyletic in these studies, Blattinae s.s. was monophyletic in some (Legendre et al. 2015; Bourguignon et al. 2018), but not in others, which placed *Archiblatta* within Blattinae s.s. (Djernæs et al. 2015; Wang et al. 2017; Evangelista et al. 2018; Liao et al. 2021).

*Protagonista* was placed deep within Blattinae as sister to the clade containing *Blatta orientalis* (Linnaeus), *Periplaneta americana* (Linnaeus), *Shelfordella lateralis* and *Neostylopyga rhombifolia* (Stoll). The separation of *Protagonista* from *Archiblatta* is consistent with the results of Wang et al. (2017) and Liao et al. (2021), the only previous phylogenetic studies to include both genera, and Bourguignon et al. (2018) placed *Protagonista* as sister to *P. americana* + *S. lateralis*. However, Wang et al. (2016) stated that the male genitalia of *Protagonista* is more similar to those of *Archiblatta* than to those of e.g. *B. orientalis*, *P. americana* and *N. rhombifolia*. Nonetheless, we



**Figure 2.** Tree showing geographical distribution of Blattoidea and classification of Blattidae into subfamilies. Within Blattidae, geographic distribution shows greater congruence with phylogeny than the ‘old’ classification does. See section 2.4. for definition of regions and Table S1 for more detailed information on distribution. The tree is from analysis C-ML-6 (Fig. 1). Both the ‘old’ classification of Blattidae and the revised classification introduced in the present paper are shown.

follow our results and those of Bourguignon et al. (2018) and include *Protagonista* in Blattinae s.s. We also tentatively include the closely related *Eroblatta* in Blattinae (see section 4.6.3.), even though it was not included in our molecular analyses. The new systematic placements for *Celatoblatta*, *Duchailluia*, *Hebardina*, *Maoriblatta* and *Pelmatosilpha* are discussed below in sections 4.6.2. (*Duchailluia* and *Hebardina*), 4.6.4. (*Celatoblatta* in part), 4.6.5.1. (*Maoriblatta*), 4.6.5.2. (*Celatoblatta* in part), 4.6.5.4. (*Celatoblatta* in part), and 4.6.6. (*Pelmatosilpha*).

Future studies should aim to increase the taxon sampling of Blattinae. This study included 13 genera placed in Blattinae s.l., five of which we moved to other subfamilies. Thus, it is quite likely that some of the remaining genera might also belong outside Blattinae s.s. One genus of particular interest is the Neotropical *Henicotyle*, as no other Blattinae s.s. are native to the New World. However, Rehn and Hebard (1927) stated that *Henicotyle* is more closely related to *B. orientalis* and *N. rhombifolia* (both typical Blattinae s.s. included in this study) than to the Neotropical genera *Eurycotis*, *Pelmatosilpha* (see section 4.6.6. for placement) or *Lamproblatta* (Lamproblattidae). The genus *Dorylaea*, found in Indo-Malaya and Australasia, is also of interest as Mackerras (1968a) stated that it probably belongs to Polyzoisteriinae.

Another genus of particular interest is *Neostylopyga*, although the type species, *N. rhombifolia*, has been included in our and several other studies. Mackerras (1968a) considered *Neostylopyga* a “heterogenous collection of species” and Anisutkin (2010) stated that the male genitalia in the genus are very variable. Thus, it is likely that *Neostylopyga* as currently defined is not monophyletic, and may contain species that do not belong in Blattinae s.s.

Another issue is the polyphyly of *Periplaneta*. The type species *P. americana* is more closely related to several other genera (*Shelfordella*, *Neostylopyga*, *Blatta* and *Protagonista*) than to *P. australasiae* (Fabricius), *P. brunnea* (Burmeister) and *P. fuliginosa* Serville. Thus, the genus, which contains several important pest species, is in dire need of a revision to clarify if the name *Periplaneta* is applicable to more species than just *P. americana*, and whether the remaining species presently included in *Periplaneta* form a monophyletic group as do at least *P. australasiae*, *P. brunnea* and *P. fuliginosa*. Furthermore, the group containing *P. australasiae*, *P. brunnea* and *P. fuliginosa* needs a new generic name.

#### 4.6.2. Duchailuiinae stat. rev.

*Duchailluia*, together with *Hebardina* in the analyses of the complete data set, was consistently placed as sister to all other Blattidae, as has been the case in previous molecular studies including *Duchailluia* (Djernæs et al. 2015, 2020; Wang et al. 2017; Evangelista et al. 2018). Based on the peculiar shape of the styli (small, non-cylindrical and furcated), Roth (2003a) moved *Duchailluia* from Blattinae to a separate subfamily, Duchailuiinae. Anisutkin and Telnov (2018) returned *Duchailluia* to

Blattinae as they considered the male genitalia ‘principally similar’.

In our analyses of the complete data set, *Hebardina concinna* was consistently placed as sister to *Duchailluia* sp. with good support (pp = 100, bs = 76–81). However, it should be noted that the placement of *Hebardina* is based on very limited data as only part of COI (barcode region) and part of COII was available for *H. concinna* and that the sequence overlap between *Duchailluia* sp. and *H. concinna* is only 352 nt.

Based on our results and those of other phylogenetic studies (see above) we reinstate Duchailuiinae, now comprised of *Duchailluia*, *Distylopyga* (restored from synonymy with *Duchailluia* by Anisutkin and Telnov 2018) and tentatively *Hebardina*. Duchailuiinae occurs in the Afrotropics and Indo-Malaya (Beccaloni 2014).

#### 4.6.3. Archiblattinae

Archiblattinae was created as a separate family level group by Walker (1868, as Planeticidae) based on unspecified differences to all other cockroaches. Kirby (1904) changed the name to Archiblattinae and included *Catara*, and Princis (1965) also included *Protagonista* and *Eroblatta* in Archiblattinae. Klass (1997) placed *Archiblatta* in Blattinae, but Roth (2003b) considered Archiblattinae a separate subfamily within Blattidae, consisting of *Archiblatta*, *Catara*, and tentatively *Protagonista*. Wang et al. (2016) studied the morphology of *Eroblatta* and *Protagonista* and included both in Archiblattinae. Thus, Archiblattinae as currently defined contains four genera: *Archiblatta*, *Catara*, *Eroblatta* and *Protagonista* (Beccaloni 2014). Of these, *Archiblatta*, *Catara* and *Protagonista* were included in the present study.

In our analyses, *Archiblatta* + *Catara* formed a clade while *Protagonista* was placed deep within Blattinae, see section 4.6.1. The last genus assigned to Archiblattinae, *Eroblatta*, has never been included in a phylogenetic study. However, the single species comprising *Eroblatta*, *E. borneensis* (Shelford), was originally described as *Protagonista borneensis* by Shelford (1908), and Wang et al. (2016) stated that *Eroblatta* and *Protagonista* are closely related, thus we tentatively return *Eroblatta* to Blattinae.

Our analyses placed *Archiblatta* + *Catara* as sister to Blattinae s.s., consistent with Legendre et al. (2015: *Archiblatta*), Evangelista et al. (2019: *Catara*), and Bläser et al. (2020: *Catara*). On the other hand, Djernæs et al. (2015), Wang et al. (2017), and Liao et al. (2021) placed *Archiblatta* as sister to *Deropeltis* (Blattinae s.s.) and Evangelista et al. (2018) placed *Archiblatta* as sister to *Deropeltis* + *Pseudoderopeltis* (both Blattinae s.s.).

Based on the available evidence, the support for retaining Archiblattinae is not very strong. On the other hand, the evidence does not clearly place Archiblattinae within Blattinae either. Most studies with a relevant taxon sampling do support a monophyletic Archiblattinae + Blattinae (Inward et al. 2007; Djernæs et al. 2015; Legendre et al. 2015; Evangelista et al. 2018, 2019; Bläser et al. 2020; Liao et al. 2021). Lacking firm evidence that Ar-

chiblattinae should be subsumed in Blattinae, we retain it as a separate subfamily, consisting of *Archiblatta* and *Catara*, which occurs in Indo-Malaya (Beccaloni 2014). Future studies might show that Archiblattinae should be subsumed in Blattinae, possibly as tribe Archiblattini, but that awaits further evidence and a better sampling of Blattinae.

#### 4.6.4. Austrostylopyginae subfam. nov.

<http://zoobank.org/62453049-1FB6-44A9-BFE6-E41CD4-0B9515>

**Type-genus.** *Austrostylopyga* Mackerras, 1968.

**Diagnosis.** See Mackerras' (1968a) diagnosis for genus *Austrostylopyga*.

In all our analyses, we found a highly supported clade (pp = 100, bs = 97–100) consisting of four species currently placed in *Celatoblatta* (Blattinae s.l.) and *Eppertia* (Polyzosteriinae). The four species were *Celatoblatta shelfordi* (Shaw), *Celatoblatta* sp. W23, *Celatoblatta* sp. W24 and *Eppertia aptera* (Princis). Our analyses generally placed this group as sister to all other Blattidae except Duchailiinae, but some analyses of the complete data set placed the group as sister to Polyzosteriinae (Table S2).

The four species in the group belong to the genus *Austrostylopyga* as defined by Mackerras (1968a); all four species were identified by JM using Mackerras (1968a). Mackerras erected *Austrostylopyga* (Blattinae) with *shelfordi* as the type species to accommodate six Australian and New Guinean species that she considered intermediate between Blattinae and Polyzosteriinae. Mackerras stated that the general appearance is very similar to *Platyzosteria* (Polyzosteriinae), but that the legs (specifically the metatarsal spines, symmetry of the pretarsal claws and shape of the femoral comb) are more similar to Blattinae. Mackerras found that the proventriculus is blattine-like while the shape of the spermatheca and L2 in the male genitalia and the laterosternal shelf in the female genitalia is polyzosteriine-like. Princis (1971) synonymised *Austrostylopyga* with *Celatoblatta*, but transferred *E. aptera* to *Eppertia* (Polyzosteriinae) instead of including it in *Celatoblatta* as he did with the other members of *Austrostylopyga*.

Based on our results, we restore *Austrostylopyga* as defined by Mackerras (1968a). However, our results do not support placing this genus in Blattinae. Furthermore, *Austrostylopyga* cannot be firmly placed within any of the existing subfamilies, neither based on our molecular results nor based on Mackerras' (1968a) morphological observations. Hence, we place *Austrostylopyga* in a separate subfamily, Austrostylopyginae, which occurs in Australia and New Guinea.

#### 4.6.5. Polyzosteriinae

Polyzosteriinae as currently defined was non-monophyletic in all our analyses, in part due to *Eurycotis* (+ *Pelmatosilpha*) being placed as sister to Archiblattinae +

Blattinae s.s., in part due to genera currently placed in Blattinae s.l. being subordinate in Polyzosteriinae (*Celatoblatta* in part, *Maoriblatta*), and due to the placement of *Macrocerca* (Macrocercinae) within Polyzosteriinae. We discuss these placements in detail in sections 4.6.6. (*Eurycotis*), 4.6.5.1. (*Maoriblatta*), 4.6.5.2. (*Celatoblatta* in part, *Macrocerca*), and 4.6.5.4. (*Celatoblatta* in part). Polyzosteriinae excluding *Eurycotis* (henceforth referred to as Polyzosteriinae) was generally divided into four clades, two of which largely corresponded to the tribes Methanini and Polyzosteriini as defined by Mackerras (1965a, 1968a). Based on this and the geographic distribution of the four clades (Fig. 2), we divide Polyzosteriinae into four tribes, see below. Our sampling of Polyzosteriinae included representatives for all genera currently included in Polyzosteriinae, except *Leptozosteria* and *Pseudolampra* (which, however, were considered by Mackerras 1966a, 1967a), and should form a solid base for future systematic and taxonomic work on the group. However, within the tribes, genera are often non-monophyletic, indicating a need for revisionary work.

##### 4.6.5.1. Polyzosteriini

The tribe Polyzosteriini was erected by McKittrick (1964) based primarily on the structure of the proventriculus in the genera *Maoriblatta* (as *Platyzosteria*), *Melanozosteria*, *Platyzosteria* and *Polyzosteria*. Mackerras (1965b, c, 1966a, b, 1967a, b, 1968b) also included *Anamesia*, *Cosmozosteria*, *Desmozosteria*, *Eppertia*, *Euzosteria*, *Leptozosteria*, *Megazosteria*, *Pseudolampra*, and *Zonioploca* in Polyzosteriini.

In our analysis, we consistently found a well-supported clade (pp 98–100, bs 73–96) containing all sampled specimens of these genera (no *Leptozosteria* or *Pseudolampra* sampled, several genera only included in complete data set, see Table S1), consistent with the results of Bourguignon et al. (2018), the only other recent study with a sizeable sampling of Polyzosteriini. Thus, we regard this clade as tribe Polyzosteriini sensu Mackerras (1968a).

However, it could be argued that *Celatoblatta* sensu Johns (1966) and the New Caledonian polyzosteriines should be included in Polyzosteriini, especially as *Maoriblatta brunni* (Alfken) is apparently both included in *Celatoblatta* sensu Johns and is one of the species that McKittrick (1964) based her definition of Polyzosteriini on (as *Platyzosteria brunni*). However, Johns (1966) specifically stated that his *Celatoblatta brunni* is not the same species as McKittrick's (1964) *Platyzosteria brunni*, which is instead a mislabelled *Maoriblatta rufoterminata* (Brunner von Wattenwyl) (then *Platyzosteria*). Additionally, some *Celatoblatta* sensu Johns have vestigial hind wings which are not found in Polyzosteriini sensu Mackerras (1965a, 1968a). Based on this, the distinct phylogenetic and geographic separation between *Celatoblatta* sensu Johns, the New Caledonian polyzosteriines and the genera included in Polyzosteriini by McKittrick (1964) and Mackerras (1965a, b, c, 1966a, b, 1967a, b, 1968b), see Figs 1, 2, we do not include *Celatoblatta* sensu Johns or the New Caledonian polyzosteriines in Polyzosteriini.

While Polyzosteriini has never been formally abolished, it has not been used much in recent years, e.g. it is presently not used by Cockroach Species File (Beccaloni 2014). We propose to reinstate it as a useful (and used) unit in cockroach taxonomy. As defined here, the distribution of Polyzosteriini is centered on Australia, but with representatives in New Zealand (*Maoriblatta*) and with some widespread *Melanozosteria* species occurring in other geographic areas (Fig. 2).

#### 4.6.5.2. Methanini stat. rev.

The tribe Methanini was erected by McKittrick (1964) based primarily on the structure of the proventriculus in *Methana*. Mackerras (1965a, 1968a) additionally placed the genera *Drymaplaneta*, *Scabina* and *Temnellytra* in Methanini based on characters from the proventriculus and the genitalia. Grandcolas (1997) considered the genitalia of the methanine genera more similar to that of *Tryonicus* than to other polyzosteriines and included these genera in his expanded Tryonicinae (then a subfamily in Blattidae) abolishing Methanini. However, Klass (2001) discussed and rejected the morphological arguments for this grouping. Tryonicinae has since been elevated to full family status containing only the genera *Tryonicus* and *Lauraesilpha* (e.g. Klass 2001; Klass and Meier 2006; Muriene 2009) and the remaining genera returned to Polyzosteriinae.

Our analyses consistently recovered a group containing all the genera included in Methanini by Mackerras (1965a, 1968a). In our analyses, this group also contained *Celatoblatta marksae* (Mackerras), which was transferred to *Celatoblatta* by Princis (1971). Our result is consistent with the results of Legendre et al. (2015) and Evangelista et al. (2018) as both of these studies placed *C. marksae* (called *Hemelytra marksae* in both studies) in a clade otherwise consisting of *Methana*, *Scabina* and *Drymaplaneta*. As *C. marksae* was originally described as *Temnellytra marksae* by Mackerras (1968a), we return this species to *Temnellytra*.

Additionally, the group containing Mackerras' (1965a, 1968a) methanines also included one or more representatives of *Macrocerca*, initially surprising as *Macrocerca* is currently placed in a separate subfamily, Macrocercinae. Although Methanini + *Macrocerca* was not supported as a clade in all analyses (see Table S2), Methanini sensu Mackerras did not form a monophyletic group exclusive of *Macrocerca* in any analyses: in analyses of the trimmed data set, a clade consisting of *Macrocerca* sp. W01, *Macrocerca* sp. W14 and *Temnellytra truncata* (Brunner von Wattenwyl) was generally sister group to the remaining methanines, and *Macrocerca* sp. W14 and *T. truncata* were always sister groups. While it is possible that our *T. truncata* is a misidentified *Macrocerca* [though not likely as even juvenile *Macrocerca* have very distinctive elongated cerci (Roth 1993)], this would not change the close relationship between Methanini and *Macrocerca* or the consistent placement of *Macrocerca* within Polyzosteriinae.

Macrocercinae was erected by Roth (1993) as he moved the genus *Macrocerca* from Blaberoidea to Blat-

tidae based on characters in the genitalia, noting a strong resemblance between the male genitalia of *Macrocerca* and many polyzosteriines. Our molecular analyses support Roth's (1993) morphology-based placement of *Macrocerca* in Blattidae, but not the placement of *Macrocerca* in a separate subfamily, Macrocercinae. Prior to Roth's placement, Princis (1965b) had placed *Macrocerca* in Blaberoidea, although Hanitsch (1930) had placed *Macrocerca* in Blattidae as close to *Periplaneta* and *Homalophilpha*. Roth (1993) stated that *Macrocerca* combines traits from both Polyzosteriinae and Blattinae and placed Macrocercinae as closer to Polyzosteriinae than to Blattinae. Roth remarked on the similarity of male genitalia and female subgenital plate between *Macrocerca* and species of Polyzosteriinae, but did not specify which trait(s) *Macrocerca* shared exclusively with Blattinae. Our results place *Macrocerca* firmly within Polyzosteriinae, and tentatively within Methanini, which is consistent with Roth's morphological assessment of the genitalia. Furthermore, a comparison of illustrations of the male genitalia of *Macrocerca browni* Roth (Roth 1993: fig. 2E) and various species of *Methana* (Mackerras 1968a: fig. 11, 13–16) reveals a striking similarity of sclerite R1 (labelled 'a' in Roth's figure), a structure that is highly variable within Polyzosteriinae. Thus, our placement of *Macrocerca* in Methanini (Polyzosteriinae) based on molecular results is, at least somewhat, supported by morphological data. Methanini as defined here occur in Australia and New Guinea (Beccaloni 2014).

#### 4.6.5.3. Rothisilphini trib. nov.

<http://zoobank.org/23A45B39-5FD0-497A-9E41-66860-02FC264>

**Type-genus.** *Rothisilpha* Grandcolas, 1997.

**Diagnosis.** 12S: occurrence of an ATTAATT motive immediately prior to the position of primer SR-N-14594 (Kambhampati and Smith 1995), a primer often used as the reverse 12S primer in molecular studies of cockroaches. COI barcode fragment: position 578 is a C and position 580 is a T or C.

In all our analyses we found a strongly supported clade (pp = 100, bs 90–100) consisting of a number of genera endemic to New Caledonia: *Rothisilpha*, *Punctulonicus*, *Pellucidionicus*, *Pallidionicus* and *Angustonicus*; all described by Grandcolas (1997). This is consistent with the results of Legendre et al. (2015) and Evangelista et al. (2018), although *Punctulonicus* and *Pellucidionicus* were not included in these studies. Previously described species included in these New Caledonian genera were formerly placed in Polyzosteriinae (Princis 1966, in *Melanozosteria*). Grandcolas (1997) placed the New Caledonian genera in Tryonicinae sensu Grandcolas (1997) together with *Methana*, *Drymaplaneta*, *Scabina*, *Temnellytra* (see section 4.6.5.2.), *Lauraesilpha* and *Tryonicus* (see section 4.4.). Beccaloni (2014) and Djernæs (2018) returned the New Caledonian genera to Polyzosteriinae based on suggestions by Muriene (2009) and Legendre et al.'s. (2015) results.

Our results as well as those of Legendre et al. (2015) and Evangelista et al. (2018) support placing *Rothsilpha*, *Punctulonicus*, *Pellucidionicus*, *Pallidionicus* and *Angustonicus* as a monophyletic group within Polyzosteriinae. Our analyses placed this group as sister to Polyzosteriini consistent with Evangelista et al. (2018), while Legendre et al. (2015) placed it as sister to Methanini. As this group of New Caledonian genera cannot be clearly placed within any of the existing subgroups of Polyzosteriinae, we classify it as a separate tribe, Rothsilphini.

In addition to Rothsilphini, nine native species of Blattidae are found in New Caledonia, currently placed in the genera *Celatoblatta*, *Maoriblatta*, *Melanozosteria*, *Platyzosteria* and *Polyzosteria*, all of the species endemic, except the two *Melanozosteria* (Beccaloni 2014). These species most likely all belong in Polyzosteriinae, although Princis (1971, 1974) placed four of these species in Blattinae, in the genera *Celatoblatta* and *Maoriblatta*. However, in this paper we have assigned these genera to Polyzosteriinae (see sections 4.6.5.1., 4.6.5.2., and 4.6.5.4.). Furthermore, prior to Princis' placement of these species, they were placed in genera now included in Polyzosteriinae [*Polyzosteria*, *Platyzosteria* and *Cutilia* (as junior synonym of *Melanozosteria*)]. Of these additional New Caledonian blattids, this study included the widespread *Melanozosteria nitida* and *Melanozosteria soror*, firmly placed in Polyzosteriini. Whether the remaining seven species should be included in Rothsilphini, or represent additional dispersal(s) from Australia (or possibly New Zealand if Princis' placement of four species in *Celatoblatta* and *Maoriblatta* is correct), will have to await further studies.

#### 4.6.5.4. Celatoblattini trib. nov.

<http://zoobank.org/1F02BE7E-315D-49F5-8F62-5C4CE0B7-B1B8>

**Type-genus.** *Celatoblatta* Johns, 1966.

**Diagnosis.** See Johns' (1966) diagnosis for genus *Celatoblatta*.

Johns (1966) erected the genus *Celatoblatta* for a number of blattid cockroaches found in New Zealand and placed it in Blattinae based on general habitus and the appearance of the legs. On the other hand, Mackerras (1968a) considered *Celatoblatta* closely related to *Temnellytra* (Polyzosteriinae: Methanini). It should be noted that Johns (1966) stated that his *Celatoblatta brunni* is not the same species as McKittrick's (1964) *Platyzosteria brunni*, see 4.6.5.1.

Princis (1970, 1971) included several species from Australia and New Guinea in *Celatoblatta*, making *Austrostylopyga* a junior synonym, and also added several species from New Caledonia. *Celatoblatta* sensu Princis was polyphyletic in all our analyses, split into three widely separated groups. One of these groups corresponds to *Celatoblatta* sensu Johns as it only contains species from New Zealand (here *Celatoblatta vulgaris*, *Celatoblatta* sp. CK77, *Celatoblatta* sp. CK109). *Celatoblatta* sensu Johns is a coherent phylogenetic group and forms

a distinctive lineage (Chinn and Gemmel 2004; Goldberg and Trewick 2011; this paper), including *C. brunni*, which was included in *Maoriblatta* by Princis (1966: p. 543), although Princis later (1967: p. 710) changed this in his corrections and placed *C. brunni* in *Celatoblatta*. We will henceforth refer to *Celatoblatta* sensu Johns as *Celatoblatta* s.s. In our analyses, *Celatoblatta* s.s. was consistently placed within Polyzosteriinae as sister to Polyzosteriini + Rothsilphini. Thus, we move *Celatoblatta* s.s. from Blattinae to Polyzosteriinae, and place it in a separate tribe, Celatoblattini, so far consisting only of *Celatoblatta* s.s. See section 4.6.5.1. for our reasons for not including Celatoblattini and Rothsilphini in Polyzosteriini.

#### 4.6.6. Eurycotiinae stat. rev.

*Eurycotis* (Polyzosteriinae) and *Pelmatosilpha* (Blattinae) were placed together in our analyses, with *Eurycotis* paraphyletic with respect to *Pelmatosilpha*. This is consistent with other studies including both *Eurycotis* and *Pelmatosilpha* (Legendre et al. 2015; Evangelista et al. 2018). Furthermore, despite their current placement in different subfamilies, the two genera have earlier been regarded as exceedingly closely related, perhaps belonging to a single genus (Rehn and Hebard 1927). However, *Eurycotis* was transferred from Blattinae to Polyzosteriinae by McKittrick (1964), who did not study *Pelmatosilpha*, which consequently remained in Blattinae.

Our analyses placed *Eurycotis* + *Pelmatosilpha* as sister to Archiblattinae + Blattinae (pp 88–100, bs < 50–81), consistent with the placement of *Eurycotis* found by Liao et al. (2021), generally with that of Wang et al. (2017), and partially consistent with the placement(s) of *Eurycotis* found by Djernæs et al. (2015). However, Legendre et al. (2015) and Evangelista et al. (2018) placed *Eurycotis* + *Pelmatosilpha* as sister to Archiblattinae + Blattinae + (remaining) Polyzosteriinae, and Inward et al., (2007), Muriene (2009), Bourguignon et al. (2018), and Bläser et al. (2020) placed *Eurycotis* (*Pelmatosilpha* not included) as sister to (the remaining) Polyzosteriinae. McKittrick (1964) moved *Eurycotis* from Blattinae to Polyzosteriinae based on similarities in the genitalia, but noted that the proventriculus and behaviour of *Eurycotis* is more similar to Blattinae. McKittrick also noted that it was odd to find members of Polyzosteriinae in the new world as this subfamily is otherwise centered in the Australasian region. McKittrick placed *Eurycotis* in a separate tribe, Eurycotiini, and considered it sister to the remaining Polyzosteriinae.

Molecular phylogenetic results do not generally support McKittrick's (1964) placement of *Eurycotis* in Polyzosteriinae, but neither do they support the previous placement of *Eurycotis* in Blattinae (see above). Our molecular results, as well as those of Legendre et al. (2015) and Evangelista et al. (2018), do support a very close relationship between *Eurycotis* and *Pelmatosilpha*. Based on this, we move *Eurycotis* from Polyzosteriinae and raise Eurycotiini to Eurycotiinae stat. rev. and we also move *Pelmatosilpha* from Blattinae to Eurycotiinae. Eurycoti-

**Table 1.** State of the art assignments to subfamily and tribe for blattid genera. Assignments are based on a synthesis of results from the present paper = Dj(tp), other recent molecular or combined phylogenetic studies with a relevant sampling of Blattidae: Inward et al. (2007) = In(07); Muriene (2009) = Mu (2009); Djernæs et al. (2015) = Dj(15); Legendre et al. (2015) = Le(15); Wang et al. (2017) = Wa(17); Bourguignon et al. (2018) = Bo(18); Evangelista et al. (2018) = Ev(18); Evangelista et al. (2019) = Ev(19); Liao et al. (2021) = Li(21). The table also includes results from the two seminal morphological studies by McKittrick (1964) = Mc(64) and Mackerras (1965a, b, c, 1966a, b, 1967a, b, 1968a, b) = Ma(65–68). Type genera of subfamilies and tribes are indicated. The names and definitions of genera generally follow the Cockroach Species File (Beccaloni 2014), but with some changes made in the present paper; this concerns the genera *Austrostylopyga* and *Eppertia* (see section 4.6.4.), *Celatoblatta* (see sections 4.6.4., 4.6.5.2., 4.6.5.4.), and *Temnellytra* (see section 4.6.5.2.). The inclusion and placement of a genus in this table does not refer to the type species, but to the species (or unidentified member(s) of a genus) studied by the authors of the relevant publication(s). <sup>1</sup> Mackerras retained *Austrostylopyga* in Blattinae, but with reservations, see section 4.6.4. <sup>2</sup> As sister to (the remaining) Polyzosteriinae. <sup>3</sup> In fig. 5. <sup>4</sup> In fig. 3. <sup>5</sup> Placement in Polyzosteriinae, no tribal assignment possible. <sup>6</sup> Placement in Polyzosteriinae outside Polyzosteriini supported. <sup>7</sup> *Temnellytra* misspelled as *Hemelytra*. <sup>8</sup> *Maoriblatta novaeseelandiae* as *Platyzosteria novaeseelandiae*. <sup>9</sup> Based on the Australian species *Maoriblatta sublobata* as *Melanozosteria sublobata*. <sup>10</sup> Placement in Polyzosteriinae outside Methanini and Rothsilphini supported.

Subfamily and tribe Assigned genera	According to study of	Taxonomic assignment in Cockroach Species File	Assignment in column 1 contradicted in	Therein resulting as
<b>Archiblattinae</b>				
<i>Archiblatta</i> (type genus)	Dj(tp), In(07), Mu(09), Le(15)	Archiblattinae	Dj(15), Wa(17), Ev(18), Li(21)	Blattinae
<i>Catara</i>	Dj(tp), Ev(19)	Archiblattinae		
<b>Austrostylopyginae</b> subfam. nov.				
<i>Austrostylopyga</i> (type genus)	Dj(tp)	Blattinae: <i>Celatoblatta</i> & Polyzosteriinae: <i>Eppertia</i>	Ma(65–68) <sup>1</sup>	Blattinae
<b>Blattinae</b>				
<i>Blatta</i> (type genus)	Dj(tp), Mc(64), In(07), Mu(09), Le(15), Bo(18), Ev(18), Li(21)	Blattinae		
<i>Cartoblatta</i>	Dj(tp)	Blattinae		
<i>Deropeltis</i>	Dj(tp), Mc(64), In(07), Mu(09), Dj(15), Le(15), Wa(17), Bo(18), Ev(18), Ev(19), Li(21)	Blattinae		
<i>Homalophilpha</i>	Dj(tp), Wa(17), Li(21)	Blattinae		
<i>Mimosilpha</i>	Li(21)	Blattinae		
<i>Neostylopyga</i>	Dj(tp), Mc(64), Le(15), Bo(18), Ev(18), Li(21)	Blattinae		
<i>Periplaneta</i>	Dj(tp), Mc(64), In(07), Mu(09), Dj(15), Le(15), Wa(17), Bo(18), Ev(18), Ev(19), Li(21)	Blattinae		
<i>Protagonista</i>	Dj(tp), Wa(17), Bo(18), Li(21)	Archiblattinae		
<i>Pseudoderopeltis</i>	Dj(tp), In(07), Mu(09), Le(15), Ev(18)	Blattinae		
<i>Shelfordella</i>	Dj(tp), In(07), Le(15), Bo(18), Ev(18), Ev(19), Li(21)	Blattinae		
<b>Duchailluinae</b> stat. rev.				
<i>Duchailluia</i> (type genus)	Dj(tp), Dj(15), Wa(17), Ev(18)	Blattinae		
<i>Hebardina</i>	Dj(tp)	Blattinae		
<b>Eurycotiinae</b> stat. rev.				
<i>Eurycotis</i> (type genus)	Dj(tp), Mc(64) <sup>2</sup> , In(07) <sup>2</sup> , Mu(09) <sup>2</sup> , Dj(15) <sup>3</sup> , Le(15), Wa(17), Bo(18) <sup>2</sup> , Ev(18), Ev(19) <sup>2</sup> , Li(21)	Polyzosteriinae	Mc(64) <sup>2</sup> , In(07) <sup>2</sup> , Mu(09) <sup>2</sup> , Dj(15) <sup>2,4</sup> , Bo(18) <sup>2</sup> , Ev(19) <sup>2</sup>	Polyzosteriinae
<i>Pelmatosilpha</i>	Dj(tp), Le(15), Ev(18)	Blattinae		
<b>Polyzosteriinae</b>				
<b>Celatoblattini</b> trib. nov.				
<i>Celatoblatta</i> (type genus)	Dj(tp)	Blattinae		
<b>Methanini</b> stat. rev.				
<i>Drymaplaneta</i>	Dj(tp), Ma(65–68), Mu(09) <sup>5</sup> , Le(15), Ev(18)	Polyzosteriinae		
<i>Macrocerca</i>	Dj(tp)	Macrocercinae		
<i>Methana</i> (type genus)	Dj(tp), Mc(64), Ma(65–68), Le(15), Bo(18) <sup>6</sup> , Ev(18)	Polyzosteriinae		
<i>Scabina</i>	Dj(tp), Ma(65–68), Le(15), Ev(18)	Polyzosteriinae		

Subfamily and tribe Assigned genera	According to study of	Taxonomic assignment in Cockroach Species File	Assignment in column 1 contradicted in	Therein resulting as
<i>Temnelytra</i>	Dj(tp), Ma(65–68), Le(15) <sup>7</sup> , Ev(18) <sup>7</sup>	Polyzosteriinae: <i>Temnelytra</i> & Blattinae: <i>Celatoblatta</i>		
<b>Rothsilphini</b> trib. nov.				
<i>Angustonicus</i>	Dj(tp), Mu(09) <sup>5</sup> , Le(15), Ev(18)	Polyzosteriinae		
<i>Pallidionicus</i>	Dj(tp), Le(15), Ev(18)	Polyzosteriinae		
<i>Pellucidonicus</i>	Dj(tp)	Polyzosteriinae		
<i>Punctulonicus</i>	Dj(tp)	Polyzosteriinae		
<i>Rothsilpha</i> (type genus)	Dj(tp), Le(15), Ev(18)	Polyzosteriinae		
<b>Polyzosteriini</b>				
<i>Anamesia</i>	Dj(tp), Ma(65–68)	Polyzosteriinae		
<i>Cosmozosteria</i>	Dj(tp), Ma(65–68), Li(21) <sup>5</sup>	Polyzosteriinae		
<i>Desmozosteria</i>	Dj(tp), Ma(65–68)	Polyzosteriinae		
<i>Eppertia</i>	Dj(tp), Ma(65–68)	Polyzosteriinae		
<i>Euzosteria</i>	Dj(tp), Ma(65–68)	Polyzosteriinae		
<i>Leptozosteria</i>	Ma(65–68)	Polyzosteriinae		
<i>Maoriblatta</i>	Dj(tp), Mc(64) <sup>8</sup> , Ma(65–68) <sup>9</sup>	Blattinae		
<i>Megazosteria</i>	Dj(tp), Ma(65–68)	Polyzosteriinae		
<i>Melanozosteria</i>	Dj(tp), Mc(64), Ma(65–68), Le(15) <sup>i</sup> , Bo(18), Ev(18) <sup>10</sup>	Polyzosteriinae	Wa(17)	Blattinae
<i>Platyzosteria</i>	Dj(tp), Mc(64), Ma(65–68), Bo(18)	Polyzosteriinae		
<i>Polyzosteria</i> (type genus)	Dj(tp), Mc(64), Ma(65–68), Bo(18), Li(21) <sup>5</sup>	Polyzosteriinae		
<i>Pseudolampra</i>	Ma(65–68)	Polyzosteriinae		
<i>Zonioploca</i>	Dj(tp), Ma(65–68)	Polyzosteriinae		

inae occurs in the New World, primarily in the Neotropic region (Beccaloni 2014).

#### 4.6.7. Relationships between blattid subfamilies

The relationships between the various subfamilies in Blattidae were generally consistent between analyses with all analyses of the trimmed data set and half the analyses of the complete data set supporting Duchailiinae + (Austrostylopyginae + (Polyzosteriinae + (Eurycotiinae + (Archiblattinae + Blattinae s.s.))), see Fig. 1 and Table S2. The remaining analyses (C-BI-4, C-BI-10, C-ML-4) instead supported Austrostylopyginae and Polyzosteriinae as sister groups, relationships otherwise as above.

The placement of Duchailiinae as sister to the remaining Blattidae (pp 98–100, bs 75–100) is consistent with other molecular studies in which it has been included (Wang et al. 2017; Evangelista et al. 2018; Djernæs et al. 2020) and with the combined molecular and morphological study of Djernæs et al. (2015). However, Anisyutkin and Telnov (2018) placed *Duchailiua* within Blattinae, although not based on any phylogenetic analysis. The placement of *Duchailiua* outside Blattinae is supported in all our analyses, with maximum support for Archiblattinae + Blattinae (excl. *Duchailiua*) in all analyses of the trimmed data set (pp 100, bs 100), but with lower bootstrap support in analyses of the complete data set (pp 97–99, bs 59–65).

The placement of Austrostylopyginae as sister to all other Blattidae except Duchailiinae (pp 82–99, bs

54–60), or alternatively, as sister to Polyzosteriinae (pp 50–58, bs < 50), are both novel placements for this group. *Austrostylopyga* has never previously been included in any phylogenetic studies. Taxonomically, it has been placed in Blattinae as genus *Austrostylopyga* (Mackerras 1968a), or mainly in Blattinae as part of *Celatoblatta* and partially in Polyzosteriinae as part of *Eppertia* Princis (1970, 1971), see section 4.6.4. for details. However, our placement of *Austrostylopyga* outside either Blattinae or Polyzosteriinae is consistent with Mackerras' (1968a) morphological observations that *Austrostylopyga* exhibit a mixture of blattine and polyzosteriine traits.

The placement of Polyzosteriinae as sister to Eurycotiinae + (Archiblattinae + Blattinae s.s.) (pp 54–72, bs < 50–65) is not generally consistent with previous studies, although it is consistent with Liao et al. (2021) and with some of the trees found by Djernæs et al. (2015). Wang et al. (2017) placed *Drymaplaneta* (Polyzosteriinae) as sister to Eurycotiinae + Archiblattinae + Blattinae, but also placed *Melanozosteria* (Polyzosteriinae) within Blattinae s.s. Legendre et al. (2015) and Evangelista et al. (2018) instead found Eurycotiinae as sister to Polyzosteriinae + (Archiblattinae + Blattinae) while Bourguignon et al. (2018), Evangelista et al. (2019), and Bläser et al. (2020) placed Polyzosteriinae + Eurycotiinae as sister to Archiblattinae + Blattinae (Archiblattinae not included in the former).

The close relationship between Archiblattinae and Blattinae s.s. is supported by all studies with a relevant taxon sampling (Inward et al. 2007; Djernæs et al. 2015; Legendre et al. 2015; Wang et al. 2017; Evangelista et



al. 2018, 2019; Bläser et al. 2020; Liao et al. 2021), but studies differ as to whether Archiblattinae and Blattinae s.s. were placed as sister groups (Inward et al. 2007; Legendre et al. 2015; Evangelista et al. 2019) or Archiblattinae were placed within Blattinae s.s. (Djernæs et al. 2015; Wang et al. 2017; Evangelista et al. 2018; Liao et al. 2021).

## 5. Conclusion

The relationship we found between the major lineages of Blattoidea (Lamproblattidae + (Blattidae + (Anaplectidae + (Tryonicidae + (Cryptocercidae + Isoptera)))) is consistent with one of the topologies found by Djernæs et al. (2015: fig. 3), but not with any other previous study including all these lineages. However, the topology was consistent between all analyses, which is in contrast to several previous studies (Djernæs et al. 2015; Wang et al. 2017; Evangelista et al. 2018). The consistency between analyses might be due to the increased taxon sampling, especially of Lamproblattidae and Tryonicidae.

Future studies should aim to increase the taxon sampling of Anaplectidae, Lamproblattidae and Tryonicidae. African *Anaplecta* species are of special interest, as are the lamproblattid genera *Lamproglanidifera* and *Eurycanthablatta* as neither have been included in a modern phylogenetic study. Within Tryonicidae, the Australian taxa should be better sampled as this study revealed a deep split within these.

Within Blattidae, we found that the current division into Archiblattinae, Blattinae, Macrocerinae and Polyzosteriinae did not agree with the phylogenetic results of this and other recent studies. We thus revised the systematics of Blattidae, dividing the family into Duchailiinae stat. rev., Austrostylopyginae subfam. nov., Eurycotiinae stat. rev., Archiblattinae, Blattinae and Polyzosteriinae. We subsumed Macrocerinae in Polyzosteriinae, and moved a number of genera from Archiblattinae, Blattinae and Polyzosteriinae.

Within Polyzosteriinae, we recovered clades largely consistent with the tribes Methanini and Polyzosteriini as defined by McKittrick (1964) and Mackerras (1965a, b, c, 1966a, b, 1967a, b, 1968a, b) with *Macrocerca* included in the methanine clade. Furthermore, we found two additional clades, one endemic to New Zealand and one endemic to New Caledonia. Thus, we divided Polyzosteriinae into Polyzosteriini, Methanini stat. rev., Celatoblatini trib. nov. and Rotherisilphini trib. nov.

Our revised classification of Blattidae will hopefully form a firm foundation for future work, but our findings also highlight the need to sample additional genera and species especially in Blattinae as additional blattid lineages are likely to be placed here.

In addition to increased taxon sampling, better data coverage is also desirable. Recent advances in getting genomic data from museum specimens (e.g. Patzold et al. 2020; Twort et al. 2021) offers intriguing possibilities of

getting overwhelmingly better data coverage from species/groups that are mainly available as older material.

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## 7. References

- Anisyutkin LN (2010) New data on the genus *Neostylopyga* Shelford, 1911 (Dictyoptera, Blattidae) with description of a new species from Laos. *Entomological Review* 90(7): 871–876. <https://link.springer.com/article/10.1134/S0013873810070055>
- Anisyutkin LN, Telnov D (2018) New data on the cockroaches previously attributed to the genus *Duchailluia* Rehn, 1933 (Dictyoptera: Blattidae: Blattinae). *Zootaxa* 4532(4): 523–538. <https://doi.org/10.11646/zootaxa.4532.4.4>
- Bai Q, Wang L, Wang Z, Lo N, Che Y (2018) Exploring the diversity of Asian *Cryptocercus* (Blattodea: Cryptocercidae): species delimitation based on chromosome numbers, morphology and molecular analysis. *Invertebrate Systematics* 32(1): 69–91. <https://doi.org/10.1071/IS17003>
- Beccaloni GW (2014) Cockroach Species File Online. Version 5.0/5.0. <http://Cockroach.SpeciesFile.org> [accessed November 2020].
- Beccaloni G, Eggleton P (2013) Order Blattodea. *Zootaxa* 3703(1): 46–48. <https://doi.org/10.11646/zootaxa.3703.1.10>
- Bläser M, Misof B, Predel R (2020) The power of neuropeptide precursor sequences to reveal phylogenetic relationships in insects: A case study on Blattodea. *Molecular Phylogenetics and Evolution* 143: 106686, 8 pp. <https://doi.org/10.1016/j.ympev.2019.106686>
- Bourguignon T, Lo N, Cameron SL, Šobotník J, Hayashi Y, Shigenobu S, Watanabe D, Roisin Y, Miura T, Evans TA (2014) The evolutionary history of termites as inferred from 66 mitochondrial genomes. *Molecular Biology and Evolution* 32(2): 406–421. <https://doi.org/10.1093/molbev/msu308>
- Bourguignon T, Tang Q, Ho SYW, Juna F, Wang Z, Arab DA, Cameron SL, Walker J, Rentz D, Evans TA, Lo N (2018) Transoceanic dispersal and plate tectonics shaped global cockroach distributions: Evidence from mitochondrial phylogenomics. *Molecular Biology and Evolution* 35(4): 970–983. <https://doi.org/10.1093/molbev/msy013>
- Bucek A, Šobotník J, He S, Shi M, McMahon DP, Holmes EC, Roisin Y, Lo N, Bourguignon T (2019) Evolution of termite symbiosis informed by transcriptome-based phylogenies. *Current Biology* 29(21): 3728–3734. <https://doi.org/10.1016/j.cub.2019.08.076>
- Cameron SL, Lo N, Bourguignon T, Svenson GJ, Evans TA (2012) A mitochondrial genome phylogeny of termites (Blattodea: Termitoidea): robust support for interfamilial relationships and molecular synapo-

- morphies define major clades. *Molecular Phylogenetics and Evolution* 65(1): 163–173. <https://doi.org/10.1016/j.ympev.2012.05.034>
- Che Y, Wang D, Shi Y, Du X, Zhao Y, Lo N, Wang Z (2016) A global molecular phylogeny and timescale of evolution for *Cryptocercus* woodroaches. *Molecular Phylogenetics and Evolution* 98: 201–209. <https://doi.org/10.1016/j.ympev.2016.02.005>
- Che Y, Bai Q, Deng W, Liao S, He J, Ho SYW, Wang Z (2020) Uplift-driven diversification revealed by the historical biogeography of the cockroach *Cryptocercus* Scudder (Blattodea: Cryptocercidae) in eastern Asia. *Systematic Entomology* 45(1): 60–72. <https://doi.org/10.1111/syen.12379>
- Chinn WG, Gemmell NJ (2004) Adaptive radiation within New Zealand endemic species of the cockroach genus *Celatoblatta* Johns (Blattidae): a response to Plio-Pleistocene mountain building and climate change. *Molecular Ecology* 13(6): 1507–1518. <https://doi.org/10.1111/j.1365-294X.2004.02160.x>
- Deng W, Liu Y, Wang Z, Che Y (2020) Eight new species of the genus *Anaplecta* Burmeister, 1838 (Blattodea: Blattoidea: Anaplectidae) from China based on molecular and morphological data. *European Journal of Taxonomy* 720: 77–106. <https://doi.org/10.5852/ejt.2020.720.1117>
- Djernaes M, Klass K-D, Picker MP, Damgaard J (2012) Phylogeny of cockroaches (Insecta, Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling. *Systematic Entomology* 37(1): 65–83. <https://doi.org/10.1111/j.1365-3113.2011.00598.x>
- Djernaes M, Klass K-D, Eggleton P (2015) Identifying possible sister groups of Cryptocercidae + Isoptera: A combined molecular and morphological phylogeny of Dictyoptera. *Molecular Phylogenetics and Evolution* 84: 284–303. <https://doi.org/10.1016/j.ympev.2014.08.019>
- Djernaes M, Varadinová ZK, Kotyk M, Eulitz U, Klass K-D (2020) Phylogeny and life history evolution of Blaberoidea (Blattodea). *Arthropod Systematics and Phylogeny* 78: 29–67. <https://doi.org/10.26049/ASP78-1-2020-03>
- Evangelista D, Thouzé F, Kohli MK, Lopez P, Legendre F (2018) Topological support and data quality can only be assessed through multiple tests in reviewing Blattodea phylogeny. *Molecular Phylogenetics and Evolution* 128: 112–122. <https://doi.org/10.1016/j.ympev.2018.05.007>
- Evangelista DA, Wipfler B, Béthoux O, Donath A, Fujita M, Kohli MK, Legendre F, Liu S, Machida R, Misof B, Peters RS, Podsiadlowski L, Rust J, Schuette K, Tollenaar W, Ware JL, Wappler T, Zhou X, Meusemann K, Simon S (2019) An integrative phylogenomic approach illuminates the evolutionary history of cockroaches and termites (Blattodea). *Proceedings of the Royal Society B: Biological Sciences* 286: 20182076, 9 pp. <https://doi.org/10.1098/rspb.2018.2076>
- Evangelista D, Simon S, Wilson MM, Kawahara AY, Kohli MK, Ware JL, Wipfler B, Béthoux O, Grandcolas P, Legendre F (2020) Assessing support for Blaberoidea phylogeny suggests optimal locus quality. *Systematic Entomology* 46(1): 157–171. <https://doi.org/10.1111/syen.12454>
- Folmer O, Black M, Hoeh W, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.
- Fritzsche I, Zompro O, Adis J (2008) A remarkable “ancient” cockroach from Brazil (Insecta: Oothecariformia: Blattodea: Blattidae: Cryptocercinae). *Arthropoda* 16(2): 34–37.
- Giribet G, Carranza S, Bagnà J, Riutort M, Ribera C (1996) First molecular evidence for the existence of a Tardigrada + Arthropoda clade. *Molecular Biology and Evolution* 13(1): 76–84. <https://doi.org/10.1093/oxfordjournals.molbev.a025573>
- Goldberg J, Trewick SA (2011) Exploring phylogeographic congruence in a continental island system. *Insects* 2(3): 369–399. <https://doi.org/10.3390/insects2030369>
- Grandcolas P (1997) Systématique phylogénétique de la sous-famille des Tryonicinae (Dictyoptera, Blattaria, Blattidae). In: Najt J, Matile L (Eds) *Zoologia Neocaledonica*, vol. 4. Mémoires du Muséum National d’Histoire Naturelle, Paris 171: 91–124.
- Hanitsch R (1930) Blattidae collected by HRH Prince Leopold of Belgium during a tour in the east. Preliminary diagnoses. *Bulletin et Annales de la Société Entomologique Belgique* 70: 254–262.
- Hebard M (1919) Studies in the Dermaptera and Orthoptera of Colombia. First paper. Dermaptera and orthopterous families Blattidae, Mantidae and Phasmidae. *Transactions of the American Entomological Society* 45(2): 89–179.
- Hebard M (1926) The Blattidae of French Guiana. *Proceedings of the Academy of Natural Sciences of Philadelphia* 78: 135–244.
- Inward D, Beccaloni G, Eggleton P (2007) Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters* 3(3): 331–335. <https://doi.org/10.1098/rsbl.2007.0102>
- Johns P (1966) The Cockroaches of New Zealand. *Records of the Canterbury Museum* 8: 93–136.
- Kainer D, Lanfear R (2015) The effects of partitioning on phylogenetic inference. *Molecular Biology and Evolution* 32(6): 1611–1627. <https://doi.org/10.1093/molbev/msv026>
- Kambhampati S (1995) A phylogeny of cockroaches and related insects based on DNA sequence of mitochondrial ribosomal RNA genes. *Proceedings of the National Academy of Sciences* 92(6): 2017–2020. <https://doi.org/10.1073/pnas.92.6.2017>
- Katoh K, Kuma K, Toh H, Miyata T (2005) MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* 33(2): 511–518. <https://doi.org/10.1093/nar/gki198>
- Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in bioinformatics* 20(4): 1160–1166. <https://doi.org/10.1093/bib/bbx108>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30(4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kambhampati S, Smith PT (1995) PCR primers for the amplification of four insect mitochondrial gene fragments. *Insect molecular biology* 4(4): 233–236. <https://doi.org/10.1111/j.1365-2583.1995.tb00028.x>
- Kirby WF (1904) A Synonymic Catalogue of Orthoptera. Vol. I: Orthoptera Euplexoptera, Cursoria, et Gressoria. (Forficulidae, Hemimeridae, Blattidae, Mantidae, Phasmidae). British Museum, London, 501 pp.
- Klass K-D (1995) Die Phylogenie der Dictyoptera. Dissertation zur Erlangung des Doktorgrades, Universität München, Cuvillier Verlag, Göttingen.
- Klass K-D (1997) The external male genitalia and the phylogeny of Blattaria and Mantodea. *Bonner Zoologische Monographien* 42: 1–341.
- Klass K-D (2001) Morphological evidence on blattarian phylogeny: “phylogenetic histories and stories” (Insecta, Dictyoptera). *Deut-*

- sche Entomologische Zeitschrift 48(2): 223–265. <http://dx.doi.org/10.1002/mmnd.4800480203>
- Klass K-D, Meier R (2006) A phylogenetic analysis of Dictyoptera based on morphological characters. *Entomologische Abhandlungen* 63(1–2): 3–50.
- Legendre F, Grandcolas P (2018) The evolution of sociality in termites from cockroaches: A taxonomic and phylogenetic perspective. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* 330(5): 279–287. <https://doi.org/10.1002/jez.b.22812>
- Legendre F, Nel A, Svenson GJ, Robillard T, Pellens R, Grandcolas P (2015) Phylogeny of Dictyoptera: dating the origin of cockroaches, praying mantises and termites with molecular data and controlled fossil evidence. *Plos one* 10(7): e0130127, 27 pp. <https://doi.org/10.1371/journal.pone.0130127>
- Liao S, Wang Y, Jin D, Chen R, Wang Z, Che Y (2021) Exploring the relationship of *Homalophilpa* and *Mimosilpha* (Blattodea, Blattidae, Blattinae) from a morphological and molecular perspective, including a description of four new species. *PeerJ* 9: e10618, 27 pp. <https://doi.org/10.7717/peerj.10618>
- Lo N, Luykx P, Santoni R, Beninati T, Bandi C, Casiraghi M, Wen-Hua L, Zakharov EV, Nalepa CA (2006) Molecular phylogeny of *Cryptocercus* wood-roaches based on mitochondrial COII and 16S sequences, and chromosome numbers in Palearctic representatives. *Zoological Science* 23(4): 393–398. <https://doi.org/10.2108/zsj.23.393>
- Mackerras MJ (1965a) Australian Blattidae (Blattodea) I. General remarks, and revision of the genus *Polyzosteria* burmeister. *Australian Journal of Zoology* 13(5): 841–882. <https://doi.org/10.1071/ZO9650841>
- Mackerras MJ (1965b) Australian Blattidae (Blattodea) II. Revision of the genus *Euzosteria* Shelford. *Australian Journal of Zoology* 13(5): 883–902. <https://doi.org/10.1071/ZO9650883>
- Mackerras MJ (1965c) Australian Blattidae (Blattodea) III. Revision of the genera *Zonioploca* Stal and *Eppertia* Shaw. *Australian Journal of Zoology* 13(5): 903–928. <https://doi.org/10.1071/ZO9650903>
- Mackerras MJ (1966a) Australian Blattidae (Blattodea) V. Revision of the genera *Anamesia* Tepper and *Pseudolampra* Tepper. *Australian Journal of Zoology* 14(2): 335–363. <https://doi.org/10.1071/ZO9660335>
- Mackerras MJ (1966b) Australian Blattidae (Blattodea) IV. *Megazosteria*, gen. nov., and revision of the genus *Desmozosteria* Shelford. *Australian Journal of Zoology* 14(2): 305–334. <https://doi.org/10.1071/ZO9660305>
- Mackerras MJ (1967a) Australian Blattidae (Blattodea) VII. The *Platyzosteria* group; general remarks and revision of the subgenera *Platyzosteria* Brunner and *Leptozosteria* Tepper. *Australian Journal of Zoology* 15(6): 1207–1298. <https://doi.org/10.1071/ZO9671207>
- Mackerras MJ (1967b) Australian Blattidae (Blattodea) VI. Revision of the genus *Cosmozosteria* Stål. *Australian Journal of Zoology* 15(3): 593–618. <https://doi.org/10.1071/ZO9670593>
- Mackerras MJ (1968a) Australian Blattidae (Blattodea) IX. Revision of the Polyzosteriinae tribe Methanini, Tryonicinae, and Blattinae. *Australian Journal of Zoology* 16(3): 511–575. <https://doi.org/10.1071/ZO9680511>
- Mackerras MJ (1968b) Australian Blattidae (Blattodea) VIII. The *Platyzosteria* group; subgenus *Melanozosteria* Stål. *Australian Journal of Zoology* 16(2): 237–331. <https://doi.org/10.1071/ZO9680237>
- Maddison WP, Maddison DR (2015) Mesquite: A modular system for evolutionary analysis. Version 3.03. <http://mesquiteproject.org>
- McKittrick FA (1964) Evolutionary studies of cockroaches. *Memoirs of the Cornell University Agricultural Experiment Station* 389: 1–197.
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES science gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, 1–8.
- Minh BQ, Lanfear R, Ly N-T, Trifinopoulos J, Schrempf D, Schmidt HA (2021) IQ-TREE version 2.1.2: Tutorials and Manual Phylogenomic software by maximum likelihood. <http://www.iqtree.org/doc/iqtree-doc.pdf>
- Murienne J (2009) Molecular data confirm family status for the *Tryonicus-Lauraesilpha* group (Insecta: Blattodea: Tryonicidae). *Organisms Diversity & Evolution* 9(1): 44–51. <https://doi.org/10.1016/j.ode.2008.10.005>
- Murienne J, Pellens R, Grandcolas P (2008) Short-range endemism in New Caledonia. New species and distribution of the genus *Lauraesilpha* Grandcolas, 1997 (Insecta, Dictyoptera, Blattidae, Tryonicinae). *Mémoires du Muséum national d'Histoire naturelle* 197: 261–271.
- Nunn GB, Theisen BF, Christensen B, Arctander P (1996) Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. *Journal of Molecular Evolution* 42: 211–223. <https://doi.org/10.1007/BF02198847>
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoureux JF, Wetzel WW, Hedao P, Kassem KR (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51(11): 933–938. [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]-2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]-2.0.CO;2)
- Patzold F, Zilli A, Hundsdoerfer AK (2020) Advantages of an easy-to-use DNA extraction method for minimal-destructive analysis of collection specimens. *PloS one*, 15(7): e0235222, 24 pp. <https://doi.org/10.1371/journal.pone.0235222>
- Princis K (1954) Australian Blattariae. *Lunds Universitets Årsskrift* (2) 50(13): 1–49.
- Princis K (1965a) Blattariae: Subordo Blaberoidea: Fam.: Oxyhaloidea, Panesthiidae, Cryptocercidae, Choriseuridae, Oulopterygidae, Diplopteridae, Anaplectidae, Archiblattidae, Nothoblattidae. In: Beier M (Ed) *Orthopterorum Catalogus, Pars 7*. W. Junk, 's-Gravenhage, 284–400.
- Princis K (1965b) Kleine Beiträge zur Kenntnis der Blattarien und ihrer Verbreitung. VIII (Orthoptera). *Eos* 41: 135–156.
- Princis K (1966) Blattariae: Subordo Blattoidea. Fam.: Blattidae, Nocticolidae. In: Beier M (Ed) *Orthopterorum Catalogus, Pars 8*. W. Junk, 's-Gravenhage, 402–614.
- Princis K (1967) Blattariae: Subordo Epilamproidea. Fam.: Nyctiboridae, Epilampridae. In: Beier M (Ed) *Orthopterorum Catalogus, Pars 11*. W. Junk, 's-Gravenhage, 617–710.
- Princis K (1970) Blattarien von den Inseln Rennell und Bellona. *The Natural History of Rennell Island, British Solomon Islands* 6: 31–37.
- Princis K (1971) Blattariae: Subordo Epilamproidea. Fam.: Ectobiidae. In: Beier M (Ed) *Orthopterorum Catalogus, Pars 14*. W. Junk, 's-Gravenhage, 1041–1224.
- Princis K (1974) Ergebnisse der Österreichischen Neukaledonien-Expedition 1965: Blattariae – Schaben. *Annalen des Naturhistorischen Museums in Wien* 78: 513–521.
- Rehn JAG (1930) New or little known neotropical Blattidae (Orthoptera). Number two. *Transactions of the American Entomological Society* 56: 19–71.

- Rehn JAG, Hebard M (1927) The Orthoptera of the West Indies: Number 1. Blattidae. Bulletin of the American Museum of Natural History 54(1): 1–320.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ronquist F, Huelsenbeck J, Teslenko M, Zhang C, Nylander JAA (2020) MrBayes version 3.2 Manual: Tutorials and Model summaries. Version: July 2020. [https://raw.githubusercontent.com/NBISweden/MrBayes/develop/doc/manual/Manual\\_MrBayes\\_v3.2.pdf](https://raw.githubusercontent.com/NBISweden/MrBayes/develop/doc/manual/Manual_MrBayes_v3.2.pdf)
- Roth LM (1987) The genus *Tryonicus* Shaw from Australia and New Caledonia (Dictyoptera: Blattidae: Tryonicinae). Memoirs of the Queensland Museum 25(1): 151–167.
- Roth LM (1993) The genus *Macrocercera* Hanitsch with descriptions of new species (Blattaria, Blattidae: Macrocercinae, subfam. n.). Insect Systematics and Evolution 24(3): 343–360. [https://brill.com/view/journals/ise/24/3/article-p343\\_6.xml](https://brill.com/view/journals/ise/24/3/article-p343_6.xml)
- Roth LM (2003a) Some cockroaches from Africa and islands of the Indian Ocean, with descriptions of three new species (Blattaria). Transactions of the American Entomological Society 129(1): 163–182. <https://www.jstor.org/stable/25078802>
- Roth LM (2003b) Systematics and phylogeny of cockroaches (Dictyoptera: Blattaria). Oriental Insects 37(1): 1–186. <https://doi.org/10.1080/00305316.2003.10417344>
- Shelford R (1908) On new genera and species of Blattidae. The Annals and Magazine of Natural History 8(1): 157–177.
- Shelford R (1912) New Blattidae from New-Guinea. Entomologische Rundschau 29: 51–52.
- Simon S, Letsch H, Bank S, Buckley TR, Donath A, Liu S, Machida R, Meusemann K, Misof B, Podsiadlowski L, Zhou X, Wipfler B, Bradler S (2019) Old World and New World Phasmatodea: phylogenomics resolve the evolutionary history of stick and leaf insects. Frontiers in Ecology and Evolution 7: 345, 14 pp. <https://doi.org/10.3389/fevo.2019.00345>
- Stamakis A (2008) The RAxML 7.0.4 Manual. [https://www.researchgate.net/publication/260275125\\_The\\_RAxML\\_704\\_manual](https://www.researchgate.net/publication/260275125_The_RAxML_704_manual)
- Svenson GJ, Whiting MF (2004) Phylogeny of Mantodea based on molecular data: evolution of a charismatic predator. Systematic Entomology 29(3): 359–370. <https://doi.org/10.1111/j.0307-6970.-2004.00240.x>
- Svenson GJ, Whiting MF (2009) Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the roles of Gondwanan vicariance and morphological convergence. Cladistics 25(5): 468–514. <https://doi.org/10.1111/j.1096-0031.2009.00263.x>
- Twort VG, Minet J, Wheat CW, Wahlberg N (2021) Museomics of a rare taxon: placing Whalleyanidae in the Lepidoptera Tree of Life. Systematic Entomology 46(4): 926–937.
- Walker F (1868) Catalogue of the Specimens of Blattariae in the Collection of the British Museum. British Museum, London, 239 pp.
- Wang C, Wang Z, Che Y (2016) *Protagonista lugubris*, a cockroach species new to China and its contribution to the revision of genus *Protagonista*, with notes on the taxonomy of Archiblattinae (Blattodea, Blattidae). ZooKeys 574: 57–73. <https://doi.org/10.3897/zookeys.574.7111>
- Wang Z, Shi Y, Qiu Z, Che Y, Lo N (2017) Reconstructing the phylogeny of Blattodea: robust support for interfamilial relationships and major clades. Scientific Reports 7: 3903, 8 pp. <https://doi.org/10.1038/s41598-017-04243-1>
- Whiting MF, Carpenter JM, Wheeler QD, Wheeler WC (1997) The Strepsiptera problem: phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. Systematic Biology 46(1): 1–68. <https://doi.org/10.1093/sysbio/46.1.1>
- Wu L-W, Bourguignon T, Šobotník J, Wen P, Liang W-R, Li H-F (2018) Phylogenetic position of the enigmatic termite family Stylotermitidae (Insecta: Blattodea). Invertebrate Systematics 32(5): 1111–1117. <https://doi.org/10.1071/IS17093>
- Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence data sets under the maximum likelihood criterion. PhD Thesis, University of Texas, Austin, Texas. <https://repositories.lib.utexas.edu/bitstream/handle/2152/2666/zwickld81846.pdf?sequence=2>

## Supplementary material 1

### Table S1

**Authors:** Djernæs M, Murienne J (2022)

**Data type:** .xlsx

**Explanation note:** Taxa included in the phylogenetic analyses with GenBank accession numbers.

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**Link:** <https://doi.org/10.3897/asp.80.e75819.suppl1>

## Supplementary material 2

### Table S2

**Authors:** Djernæs M, Murienne J (2022)

**Data type:** .xlsx

**Explanation note:** Clade support for relevant clades from the various analyses.

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**Link:** <https://doi.org/10.3897/asp.80.e75819.suppl2>

## Supplementary material 3

### Figures S1–S12

**Authors:** Djernæs M, Murienne J (2022)

**Data type:** .pdf

**Explanation note:** **Figure S1.** T-BI-4 tree. — **Figure S2.** T-BI-6 tree. — **Figure S3.** T-BI-10 tree. — **Figure S4.** C-BI-4 tree. — **Figure S5.** C-BI-6 tree. — **Figure S6.** C-BI-10 tree. — **Figure S7.** T-ML-4 bootstrap tree. — **Figure S8.** T-ML-6 bootstrap tree. — **Figure S9.** T-ML-10 bootstrap tree. — **Figure S10.** C-ML-4 bootstrap tree. — **Figure S11.** C-ML-6 bootstrap tree. — **Figure S12.** C-ML-10 bootstrap tree.

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