Phylogenomics and deep convergence in cockroach hind-wing morphology

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Abstract

Despite regular advances in Blattodea systematics, several relationships remain controversial or untested in formal phylogenetic reconstructions. This common situation for understudied metazoan groups limits our power to answer questions about phenotypic evolution. In this study, we infer the evolutionary history of Blattodea using newly sampled taxa that improve phylogenetic resolution while also illuminating the evolutionary history of an unusual phenotype—the apically folded hind-wing. Taxa newly sequenced include those with a hind-wing apical fold (*Anaplecta pulchella*, *A. pygmaea*, *A.* sp. cf. *malaysensis*, *Diplopterina parva*, *Prosoplecta semperi*, *Anaplectoidea klossi*, and *Oulopteryx illuminata* sp. nov. that we describe herein, including its male genitalia) and other rare taxa (*Dipteretrum hamstroemi*, *Duchailluia togoensis*, *Lauraesilpha mearetoi*, *Buboblatta vlasaki*). The phylogenetic design utilizes 41 genes over 91 species in total, analyzed in a maximum likelihood and coalescent framework. To quantify the phylogenetic uncertainty of the analysis, support for various topologies is assessed. We find unambiguous support for the surprising position of Neotropical *Oulopteryx* (Oulopterygidae) as sister to New Caledonian/Australian Tryonicidae. This, and other phylogenetic findings, reveal that the apically folded hind-wing may have arisen nine times in Blattodea. Further investigations are needed, notably with an increased taxonomic sampling, to demonstrate stronger support for the placement of rogue taxa (e.g., *Anaplecta*) and to investigate the evolutionary correlates of wing evolution.

Keywords Hind-wing · Morphology · Insects · Ancestral state reconstructions · *Oulopteryx* · Oulopterygidae

Introduction

Cockroach systematic studies continue to further refine deep (e.g., Djernæs et al., 2020; Evangelista et al., 2020; Li, 2022) and recent (e.g., Beasley-Hall et al., 2021; Velez-Bravo & Daza, 2021) relationships, but several of them remain highly

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disputed, poorly supported, or simply unstudied (for examples, see Evangelista et al., 2017; Legendre & Grandcolas, 2018). A number of morphologically distinct groups have not been phylogenetically sampled with adequate taxonomic breadth, or at all. While some taxa cannot be included yet because they remain to be discovered—estimates say only ¼ of cockroach species have been described (Legendre & Grandcolas pers. comm., Beccaloni & Eggleton, 2013)—others can be included, especially with the latest advances in sequencing (Card et al., 2021). Thus, increasing taxonomic sampling remains a central challenge of obtaining a backbone phylogeny of Blattodea (Heath et al., 2008; Zwickl & Hillis, 2002). The value of downstream phylogenetic analyses, like reconstructions of phenotype, is also highly dependent on thorough sampling (Garamszegi, 2014).

One phenotypic feature of interest is the apical folding membrane of the cockroach hind-wing (Fig. S1). This is polymorphic among winged cockroaches with most species lacking a membrane between the CuP and V[s] veins (sensu Li et al., 2018), while a few species have a membrane here. The membrane is generally devoid of veins except for V[1], which provides support towards the apical most

point and lays along the folding line. The membrane can vary from a minute triangle (i.e., an "intercalated triangle"), to a large region rivaling the size of the rest of the wing (i.e., an "appendicular field"). Although the larger form is not often seen among cockroaches, it appears to be deeply conserved within a few extant clades (e.g., Anaplectidae Walker, 1868; Ectobiinae Brunner, 1865) and is present in a variety of other taxa, both contemporary (e.g., Anisyutkin, 2013) and fossilized (Anisyutkin & Gröhn, 2012). A recent review considered all forms (except *Diploptera*) of a hind-wing apical folding to be homologous and simply used the term "apical folding" to refer to such forms (Li et al., 2018). While similar structures are seen in other insects [e.g., beetles (Kukalova-Peck & Lawrence, 1993)], the precise homology of these structures is unexamined, and the authors are unaware of any examples of closely related insects (i.e., Mantodea, Alienoptera) with this hind-wing region.

The folded membrane allows for the hind-wing to extend further outwards during flight and have higher surface area. The cost of enlarged wings is mitigated by its ability to remain protected at rest through folding or rolling underneath the tegmina (Li et al., 2018). Although its function is unstudied, the added surface area from the apical wing region likely has some aerodynamic function (Wang et al., 2018). Previous phylogenetic studies have placed some important taxa with apically folded hind wings [e.g., *Diploptera* Saussure, 1864 (Evangelista et al., 2020; Legendre et al., 2017; Li, 2022), Ectobiinae (Djernæs et al., 2020; Evangelista et al., 2020; Li, 2022), *Riatia* Walker, 1868, *Chorisoneura* Brunner, 1865, *Calhypnorna* Saussure & Zehntner, 1893, *Euhypnorna* Hebard, 1921, *Theganopteryx* Brunner, 1865 (Evangelista et al., 2020), *Anaplecta* Burmeister, 1838 (Deng et al., 2023; Djernæs et al., 2020; Li, 2022)]. However, those relationships were not always strongly supported, and these taxa alone do not effectively represent the diversity of cockroaches with apically folded hind-wings.

Here, we investigate the placement of nine newly sequenced and taxonomically disparate taxa, five of which have an apically folded hind-wing: *Anaplecta*; *Anaplectoidea* Shelford, 1906; *Oulopteryx* Hebard, 1921; *Diplopterina* Princis, 1963; and *Prosoplecta* Saussure, 1864. *Anaplecta* (Anaplectidae) has been sampled previously in molecular (Bourguignon et al., 2018; Evangelista et al., 2018; Li, 2022; Wang et al., 2017), morphological (Klass & Meier, 2006), and combined data (Djernæs et al., 2015) studies, but its position has been highly controversial. On the other hand, *Anaplectoidea* has never been included in a phylogenetic study. This genus was placed in Anaplectidae before Roth (1996)'s morphological assessment placed it in Blaberoidea. *Oulopteryx* (Oulopterygidae Rehn, 1951) has also never been included in a phylogenetic study. Oulopterygidae was previously considered to be a clade of Corydioidea Saussure, 1864 (Roth, 2003), based

on non-cladistic taxonomic treatment (Hebard, 1921). Recent work by Hinkelman et al. (2020) summarizes the taxonomic history of the group and concludes that its phylogenetic position remains uncertain, but the current best hypothesis is that it is a close relative of Blattidae. Finally, *Diplopterina* and *Prosoplecta* may be less controversial in their taxonomic affiliations but are morphologically distinct, lack phylogenetic study, and bear large folded apical regions on their hind-wings.

The four remaining newly sampled taxa we include—*Buboblatta* Hebard, 1920; *Duchailluia* Rehn, 1933; *Lauraesilpha* Grandcolas, 1997; and *Dipteretrum* Rehn, 1922—do not have apically expanded hind-wings but are important for phylogenetic sampling nonetheless. *Buboblatta* is currently considered a neotropical representative of Latindiinae Handlirsch 1925 (Evangelista et al., 2019a, b, c; Hebard, 1920; Princis, 1963). Latindiinae is a poorly sampled clade (Djernæs et al., 2015; Evangelista et al., 2018; Legendre et al., 2015) that may be among the closest relatives of Nocticolidae (Wang et al., 2017), but its monophyly has not been tested through robust geographic sampling in phylogenies. *Duchailluia* is perhaps the sister to all other Blattidae Latreille, 1810 (Djernæs et al., 2015; Djernæs & Murienne, 2022), and is thus a key taxon for both the internal blattid relationships and the placement of Blattidae in Blattoidea. *Lauraesilpha* is one of only two Tryonicidae McKittrick and Mackerras, 1965 genera (Murienne, 2009), and including it should also assist in better resolution of the blattodean backbone. Tryonicidae has only been represented by a single long-branch in recent phylogenomic studies (Evangelista et al., 2020, 2019a, b, c) and has been found in varying positions in studies relying on other data (e.g., Grandcolas, 1996; Klass & Meier, 2006; Murienne, 2009; Legendre et al., 2015). Finally, *Dipteretrum* is a poorly studied genus of African Blaberoidea, which is currently unplaced within that superfamily (Cockroach Species File, accessed 2021).

In attempting to resolve these phylogenetic issues and map the evolution of the hind-wing apical field, we present a phylogenomic study of 91 species using 41 genes. We explore phylogenetic support for alternative hypotheses and varied inference methods.

Methods

Genomic data collection

Blattodea and relevant outgroups were sampled widely from previously published studies (Evangelista et al., 2019a, b, c, 2020) with eleven targeted samples added through new sequencing (Table S1). The resulting taxon sampling comprised 86 blattodean species (cockroaches and termites) and

5 outgroups. Newly sampled taxa had DNA extracted with Qiagen DNEasy kit and target-enriched genome sequencing was done using Arbor Biosciences' myReads/myBaits workflow. Probe sets used were from Evangelista et al. (2020). Paired-end 150 sequencing was done on NovaSeq S4 (Illumina Inc.).

Precleaned libraries were further cleaned in TrimGalore v. 0.4.5 (Krueger, 2017) to remove low-quality bases and trim adapters (Phred score cutoff: 20; max. trimming error rate: 0.1; min. required adapter overlap: 1 bp; min. required sequence length for both reads before a sequence pair gets removed: 20 bp). Newly sequenced libraries were assembled using Trinity RNA Seq V.2.11 (Grabherr et al., 2011) using the –no_bowtie option. All newly sequenced and previously published assembled libraries were homologized to single-copy orthologs using two methods: EggNOG (Huerta-Cepas et al., 2017) and OrthoGraph (Petersen et al., 2017). EggNOG (Huerta-Cepas et al., 2017) identifies orthologs and annotates libraries by identifying seed orthologs from pre-existing phylogenies and genomic databases. EggNOG Mapper V5.0 parameters were set to auto-adjust per query for taxonomic scope (Arthropods) and one-to-one ortholog restriction. OrthoGraph V0.7.1 (Petersen et al., 2017) identifies orthologs based on reciprocal hidden-markov searches among reference taxa. We utilized the following ODB V.10 (Kriventseva et al., 2019) reference genomes: *Blattabacterium cuenoti*, *B.* sp. *Blaberus*, *B.* sp. *Blatta*, *B.* sp. *Blattella*, *B.* sp. *Cryptocercus*, *B.* sp. *Mastotermes*, *B.* sp. *Nauphoeta*, *Blattella germanica*, *Ladona fulva*, *Pediculus humanus*, *Tribolium castaneum*, and *Zootermopsis nevadensis*. OrthoGraph options were set to default except for the following: minimum transcript length = 35, ORF extension on, ORF minimum overlap = 0.4, HMM search score threshold = 15, BLAST score threshold = 15, and MAFFT (Katoh & Toh, 2008)—any-symbol option enabled. *Blattabacterium* is a type of Flavobacteria (Kambhampati, 2010) with a specialized symbiosis with Blattodea (Patino-Navarrete et al., 2013). These were included as a way to identify sequences from non-target bacteria. Sequences with best hits to *Blattabacterium* spp. were removed.

Alignment and data preparation

We chose 15 loci from the EggNOG assemblies for which *Oulopteryx* sp. nov.—a species with an apical folded membrane and from a family never included in any phylogenetic analysis—had the greatest overlap with other species. We added 30 other loci from the OrthoGraph assemblies: 10 that had the greatest taxon coverage including *Oulopteryx* sp. nov. and the next 20 with the most overall taxon coverage. Orthologous loci were cross-checked for duplicates across orthology methods (there were four duplicates) and combined into individual files such that each taxon had a single contig of the longest possible length across each locus (some of which contained multiple non-overlapping domains). This resulted in 41 final loci.

Loci were aligned using MAFFT V7.475 (parameters localpair –maxiterate 1000 input) (Katoh & Toh, 2008) and manually fine-tuned in AliView (Larsson, 2014). Stop codons, either at the end of coding regions or erroneously placed mid-sequence, were removed, and alignments were reading-frame adjusted. Three modified sets of alignments were created (Table 1): (i) reduced, alignments reduced to only the positions with more than 40% completeness (12,508 nts); (ii) masked, alignments with apparent non-coding (intron and ribosomal DNA loops) and hard to align regions removed (37,149 nts); and (iii) reduced and masked, both of the above conditions combined (11,584 nts).

Tree reconstruction

An IQ-TREE (Nguyen et al., 2015) concatenation maximum likelihood inference was carried out on the above alignment sets. Partition blocks were assigned according to gene and codon position for protein-coding genes and gene only for rDNA sequences. IQ-TREE2 options were as follows: -m MFP -rcluster 25 -ninit 300 -ntop 100 -nbest 20 -allnni -B 1000 -bsam GENE -bnni -nstop 250. This yielded a ML tree, a consensus of all bootstrap pseudoreplicates, and all 1000 bootstrap trees.

Individual gene tree histories were also inferred using IQ-TREE (Nguyen et al., 2015) on the "Masked" alignments. The following options were used: -m MFP -rcluster 20

Table 1 Alignment statistics

Alignment	Length (nuc)	% Characters ambiguous	Missing data blocks[a]	Parsimony informative sites	# of partitions	Avg. sites per partition
Masked	37,149	65.25%	0.08%	15,409	22	700.4
Reduced	12,508	37.43%	0.31%	5885	11	535
Reduced and masked	11,584	36.80%	0.31%	5075	20	253.8

[a]A data block is a tip missing the entirety of its data for a given gene domain

-allnni -ninit 300 -ntop 100 -nbest 20 -allnni -nstop 250. The ML gene trees were then used to infer a species tree using ASTRAL 5.7.7 (Zhang et al., 2018).

We put all concatenation trees and the consensus of all bootstrap trees into a single text file and computed the overall majority-rule consensus tree (CC-Tree). Finally, we computed the majority-rule consensus of the CC-Tree and the ASTRAL tree (Conservative Sp. Tree).

Topology testing and node support

We manually grafted the CC-Tree (Grafted sp. Tree) to reflect the assumption of monophyletic Corydioidea (not including *Anaplecta*) and monophyletic Ectobiinae (*Ectobius*, *Mediastinia*, and *Ectoneura*). We then subsequently modified the Grafted sp. Tree to create 13 additional trees. Each of the 13 unique topologies tested a previously suggested hypothesis for the placement of some taxa with apical folding: *Anaplecta*, *Anaplectoidea*, *Oulopteryx*, and *Diploptera*.

All trees were compared in an approximately unbiased test (Shimodaira, 2002) (-m MFP -rcluster 25 -p -zb 10000) under both the "Masked" and "Reduced and masked" alignments along with their original partitioning block definitions. Relationship-specific tests were replicated twice, using the "Masked tree" and "Grafted sp. Tree" to estimate parameters respectively.

The final tree chosen had node support values from all three bootstrap replicates mapped onto it as well as gene concordance factors (Minh et al., 2020) calculated from the optimized gene trees.

Ancestral state reconstruction

Morphological data (Supplementary data 1) was synthesized from literature sources, databased photographs (Cockroach Species File, accessed 2021; MNHN digital collections, accessed 2021), and preserved specimens. Apical field presence was defined as any visible membranous region between the anal and anterior wing sections. This included large appendicular fields whose as basal most angle exceeded 90°, small apical triangles that are not extended enough to be the most distal point on the wing (e.g., as commonly seen in Blattellinae), and all sizes in between. Apterous and brachypterous taxa were coded as missing data.

Morphological data were analyzed in R using PhyTools (Revell, 2012). The ancestral states of categorical characters were estimated under a Bayesian framework in SIMMAP (Bollback, 2006) using the symmetrical model of evolution. The first 1000 simulations were discarded as burn-in, and 500 additional simulations were done while sampling every

10 replicates. The result was then tested for sensitivity to the phylogenetic topology. To control for phylogenetic error, each of these analyses was repeated using the eight grafted trees discussed above.

Results

Five of the eight species trees evaluated were rejected due to low *p*-values in the AU tests (Table 2). Of the remaining three trees, we chose the "Masked tree" as the best tree since both it and the consensus tree of its bootstrap trees had high lnL and *p*-values (Table 2). Although the "Reduced and Masked" tree outperformed the rest in the AUTest using the "Reduced and Masked" alignment, this test was not definitive (i.e., none of the trees were rejected as implausible), and the "Masked tree" also performed fairly well in this analysis too. Also, the "Masked tree" was obtained in an analysis with significantly more data (Table 1).

The 15 additional AU-tests definitively rejected certain relationships (Table 3). There was no support for the placement of *Anaplecta* spp. in Blaberoidea or Tryonicidae. The test also rejected the placement of *Anaplecta* spp. in a monophyletic Corydioidea. Two relationships for *Anaplecta* spp. that were supported are sister to Kittrickea or sister to *Buboblatta vlasaki* Evangelista, Kotyková-Varadínová and Jůna, 2019 (which together are sister to Blattoidea). There was no discernable signal for *Anaplectoidea* in any placement other than as sister to all remaining Blaberoidea. Similarly, no other placement for *Oulopteryx* sp. nov. was supported, other than sister to Tryonicidae. The "masked tree" was grafted with respect to the above results (Fig. 1) and was taken as the final species tree for our study.

This final topology (Fig. 1) shows a large degree of congruence with respect to the placement and monophyly of major clades in previous studies (Blaser et al., 2020; Evangelista et al., 2019a, b, c). Family-level relationships in Blaberoidea were identical to that in Evangelista et al. (2020). *Diploptera minor* (Brunner, 1865) and *Diplopterina parva* (Borg, 1902) were both placed as close relatives of *Paraplecta minutissima* (Shelford, 1908), although node support was low. *Dipteretrum hamstroemi* Princis (1963), was recovered as sister to *Supella longipalpa* (Fabricius, 1798). *Prosoplecta semperi* Shelford (1912), was recovered as closely related to *Pachnepteryx* sp. cf. *signaticollis* (Stål, 1877). Corydioidea was polyphyletic with respect to *Buboblatta vlasaki*, but the support values on this quartet are generally low. *Lauraesilpha mearetoi* Grandcolas (1997), was sister to *Tryonicus parvus* (Tepper, 1895). *Duchailluia togoensis* (Shelford, 1911) was strongly supported as sister to all other Blattidae.

Table 2 Species tree comparisons in an approximately unbiased (AU) test[a]

Tree				lnL of original tree search (not AUTest lnL)	Masked alignment		Reduced and masked alignment	
					Grafted sp. tree		Grafted sp. tree	
Name	Alignment	Software	Method		Delta LnL	*p*-value	Delta LnL	*p*-value
Reduced and masked tree	Reduced and masked	IQTree	ML	−199,935.7	47.64	0.0508	0	0.7220
Reduced and masked con. tree	Reduced and masked	IQTree	Bootstrap consensus	−199,937.8	52.16*	0.0465	0.43	0.7180
Reduced tree	Reduced	IQTree	ML	−247,225.5	138.79**	0.0018	39.3	0.0953
Reduced con. tree	Reduced	IQTree	Bootstrap consensus	−247,226.8	130.73***	0.0004	25.21	0.1800
Masked tree	Masked	IQTree	ML	−428,584.4	0	0.6750	20.43	0.1920
Masked con. tree	Masked	IQTree	Bootstrap consensus	−428,586.2	1.9	0.4960	20.72	0.1680
CC tree	-		Combined consensus	NA	53.70*	0.0456	3.21	0.3580
ASTRAL tree	Masked	IQTree+ASTRAL	Coalescence	NA	359.38***	0.0000	250.18***	0.0000

Asterisk indicates statistical significance at three levels * < 0.05; ** < 0.01; *** < 0.001

[a]Trees inferred from each alignment (maximum likelihood/ML tree and Bootstrap consensus tree) were tested against two alignments (i - masked, ii - reduced and masked) in an AU test. Tree plausibility relative to the most plausible tree is given by delta LnL values. *p*-values indicate probability that alignment could have evolved under that tree

Table 3 Topology testing

Hypothesis[a]	Masked alignment				Reduced and masked alignment			
	Masked tree		Grafted sp. tree[b]		Masked tree		Grafted sp. tree[b]	
	Delta LnL	*p*-value	Delta LnL	*p*-value	Delta LnL	*p*-value	Delta LnL	*p*-value
CC Tree	0	0.625	0	0.6	0	0.9760	0	0.9520
Grafted sp. tree[b]	15.766	0.198	14.756	0.2	30.316	0.0243	26.411	0.0483
Anaplecta is Corydioidea	34.526	0.000717	34.028	0.0	36.315	0.0035	33.069	0.0006
Anaplecta is Kittrickea	4.724	0.496	2.5681	0.5	25.852	0.0489	21.647	0.0893
Anaplecta is Blaberoidea	186.34	< 0.0001	190.04	< 0.0001	182.24	< 0.0001	179.73	< 0.0001
Anaplecta is Tryonicidae	74.162	< 0.0001	71.908	< 0.0001	64.35	0.0022	61.486	0.0017
Anaplecta and *Anaplectoidea* are Tryonicidae	367.85	< 0.0001	368.28	< 0.0001	333.55	0.0004	332.05	< 0.0001
Anaplectoidea is Solumblattodea	234.59	< 0.0001	238.61	< 0.0001	234.32	< 0.0001	232.93	< 0.0001
Anaplectoidea is Anaplectidae	233.05	< 0.0001	237.37	< 0.0001	233.43	< 0.0001	231.92	< 0.0001
Anaplectoidea is Tryonicidae	330.18	0.00147	331.24	0.0	320.69	< 0.0001	317.48	< 0.0001
Oulopteryx sp. is Anaplectidae	700.9	< 0.0001	694.58	0.0	568.65	< 0.0001	563.72	0.0008
Oulopteryx sp. is Blaberidae	1586.7	< 0.0001	1587.9	< 0.0001	1140.3	< 0.0001	1135.1	< 0.0001
Oulopteryx sp. is Blaberoidea	937.53	< 0.0001	935.7	< 0.0001	765.41	0.0001	762.07	< 0.0001
Oulopteryx sp. is Corydioidea	741.77	< 0.0001	735.53	0.0	590.44	< 0.0001	585.15	0.0002
Diploptera and *Diplopterina* are Diplopterinae	22.436	0.0284	21.486	0.0	34.717	0.0040	30.718	0.0131

[a]Last thirteen trees are modified versions of Grafted sp. tree

[b]Graft of the "CC Tree" that reflects an assumption of monophyletic Corydioidea (not including *Anaplecta*) and monophyletic Ectobiidae s.s. (*Ectobius*, *Mediastinia*, and *Ectoneura*)

Systematic entomology

Order Blattodea Brunner (1882)

Unranked Solumblattodea Evangelista and Wipfler (2019)

Super-family Blattoidea Latreille (1810)

Family Oulopterygidae Rehn (1951)

History Princis (1965) placed *Melyroidea* in Oulopterygidae with *Prosoplecta*, *Anareolaria* Shelford (1909), *Euhypnorna*, and *Oulopteryx*. Shelford's description of *Anareolaria* is not sufficient to determine its placement (Shelford, 1909), and it is currently considered unplaced
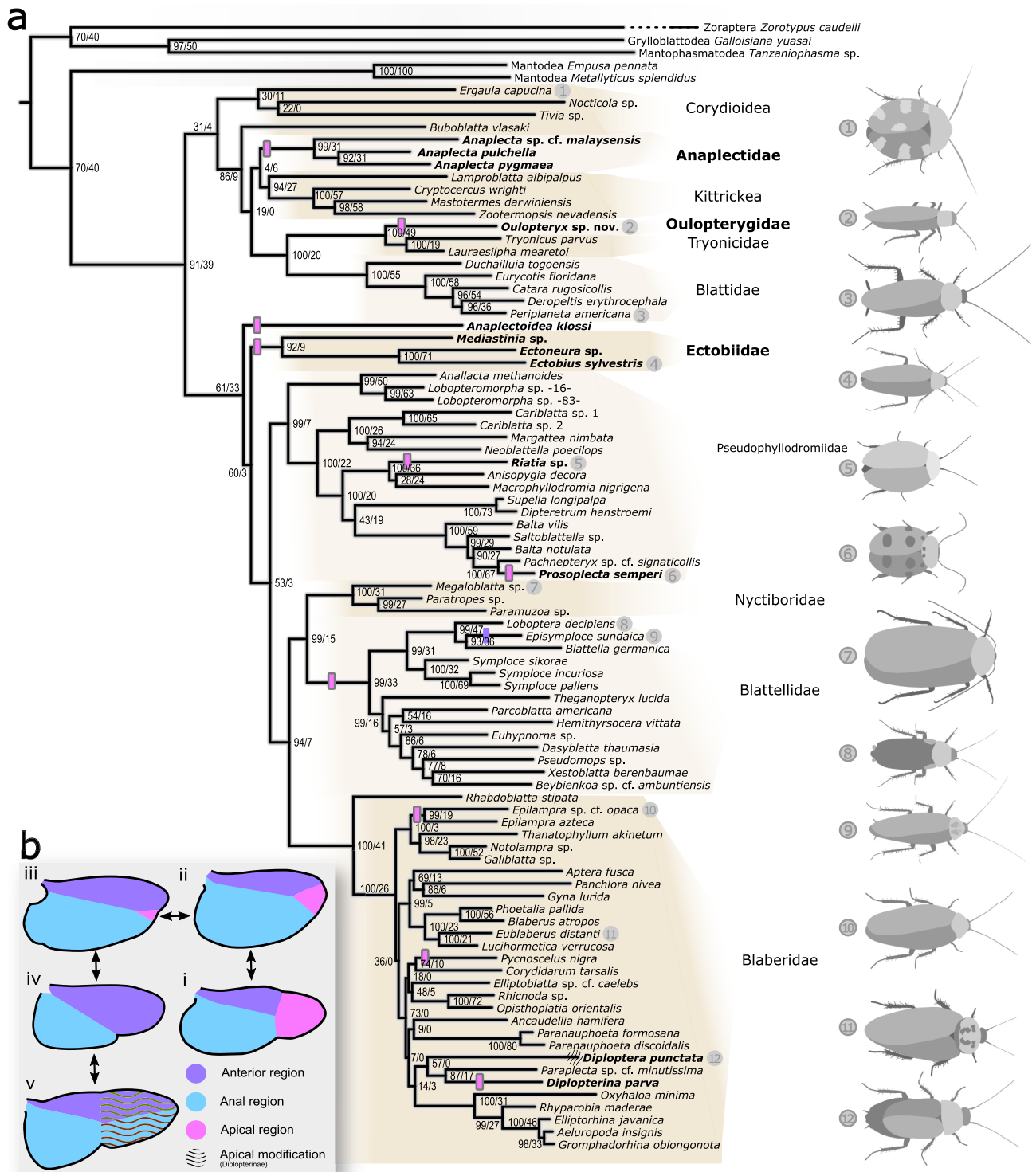
Fig. 1 Phylogeny of Blattodea (**a**) and wing morphology illustration (**b**). **a** The phylogeny presented is the final species tree resulting from a number of topology tests and inference methods (IQ-TREE and ASTRAL). Node support values represent bootstrap frequency (3000 replicates from concatenation analyses of all three modified alignments; *left*) and gene concordance factors among the 41 loci (*right*). Taxa in bold have hind wings with a very large apical folding area (**b** – i, and **b** – ii). The apical region in *Diploptera* may not be homologous to those of other taxa so we use another symbol and did not count them as addi-tional apical field gains. Symbols on branches show inferred points of apical field gain (pink with outline) and loss (purple without outline). Numbered tokens correspond to images of taxa in the corresponding clade. 1, *Therea* sp. (Corydiinae); 2, *Melyroidea magnifica* (Oulop-terygidae); 3, *Periplaneta australasiae*; 4, *Ectobius sylvestris*; 5, *Riatia orientis*; 6, *Prosoplecta semperi*; 7, *Megaloblatta longipennis*; 8, *Lobop-tera decipiens*; 9, *Episymploce asahinae*; 10, *Epilampra opaca*; 11, *Eublaberus distanti*; 12, *Diploptera punctata*

in Blaberoidea (Roth, 2003). Phylogenetic analysis (Fig. 1) clearly demonstrates that *Euhypnorna* is a genus of Blattellinae and *Prosoplecta* belongs to Pseudophyllodromiinae, placements consistent with their morphologies (Anisyutkin, 2013; Evangelista et al., 2019a, b, c). Bonfils (1975) placed *Oulopteryx* in Anaplectinae without giving a morphological justification. Roth (2003) included *Oulopteryx* in Corydioidea and *Melyroidea* in Pseudophyllodromiinae. *Aclavoidea socialis* Vidlička and Vršanský (2020) was described as being closely related to *Melyroidea* and *Oulopteryx*. However, these three oulopterygid genera have no consistent morphological differences other than body dimensions and coloration.

Family diagnosis Oulopterygidae (*Oulopteryx*, *Aclavoidea*, and *Melyroidea*) differs from Tryonicidae in the following characteristics: Neotropical distribution (as opposed to Australian), macropterous (as opposed to brachypterous), pronotum with raised anterior edge and other sculpting (as opposed to smooth and regular). Oulopterygidae differs from *Anaplecta* in the folded apical membrane of the hind-wing being rolled at rest (rather than folded). Oulopterygidae also has thicker sclerotization of body and forewings, giving it a blaberid-like appearance (as opposed to the more delicate ectobiid-like appearance of Anaplectidae).

Genus *Oulopteryx* Hebard (1921)

Included species *Oulopteryx meliponarum* Hebard (1921) (type species), *O. dascilloides* Hebard (1921), *O. illuminata* Evangelista and Legendre *sp. nov.*

Key to *Oulopteryx* species

1. Relatively large (body length > 12 mm); pronotum elliptical; pronotum, supra-anal plate and elytra without setae; pattern of hind-wing cross venation between R and M roughly parallel; interocular space roughly similar to inter-antennal space; styli half as long as distance between styli, cerci short and stout … *O. illuminata* Evangelista & Legendre sp. nov.
2. Relatively small (body length < 12 mm); pronotum nearly circular; pronotum, lateral margin of elytra and caudal margin of supra-anal plate setose; pattern of hind-wing cross venation between R and M tortuous for a few veins; interocular space distinctly smaller than inter-antennal space; styli length 1/3 of distance between styli; cerci relatively long and slender … *O. meliponarum* Hebard (1921)
3. Relatively small (body length < 12 mm); pronotum and elytra without setae; supra-anal plate setose; pattern of

hind-wing cross venation between R and M roughly parallel; interocular space slightly smaller than inter-antennal space; styli length 1/3 of distance between styli; cerci short and stout … *O. dascilloides* Hebard (1921)

Species *Oulopteryx illuminata* Evangelista and Legendre sp. nov.

[Zoobank LSID: lsid:zoobank.org:act:0845FCB3-D4C6-440A-B0D3-D90A3E94E350]
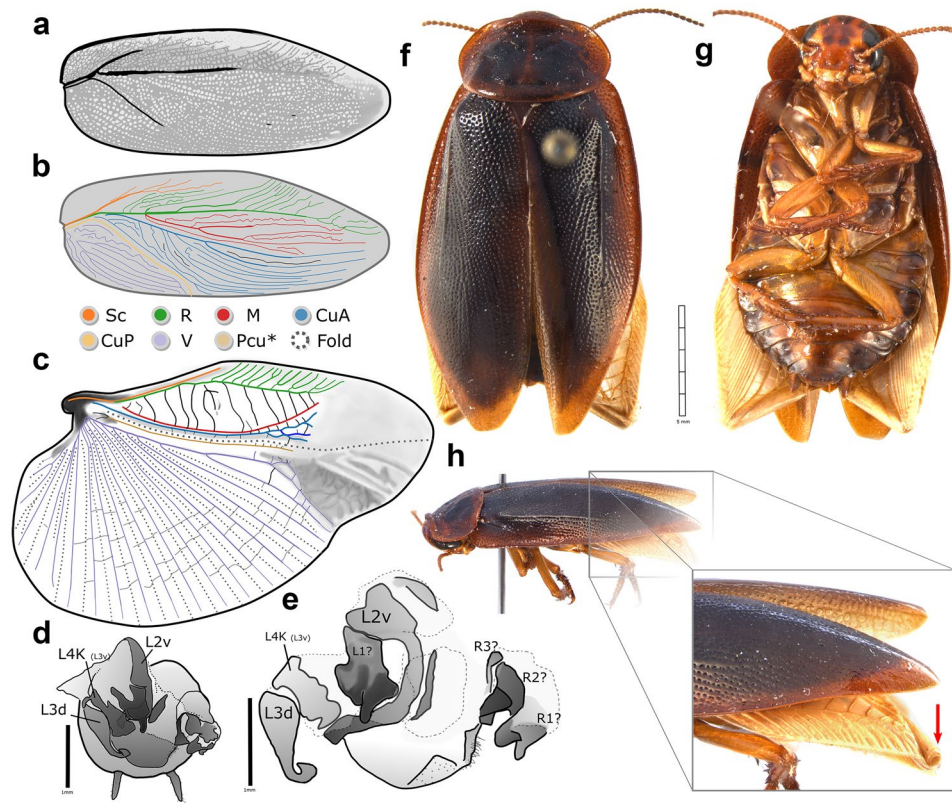
(Fig. 2)

Type material Holotype male: OUMNH-2005-065; Evergreen Forest, 1080 m alt.; @ M.V. light; coll. Mann, Hamel & Simmons.

Type locality BOLIVIA: Dep. Santa Cruz; Bermejo, Refugio Los Volcanes, 18°06'S 63°36'W.

Description (male, female unknown) General color reddish-chestnut. Head (Fig. 2g) large and round, yellow–brown, frons darker as well as four dark brown stripes on the vertex; clypeus unipartite but two-colored (tip hyaline); eyes black, bean-shaped; ocelli absent; maxillary palps five-segmented with the first two segments short, the third one the longest (ca. three times longer than the second one), the fourth segment half as long as the third, the fifth segment enlarged, oval, with fine setae mostly on the edges; interocular space slightly larger than inter-antennal space; antennae brown, darker at their tips, scape as long as the first two antennomeres. Pronotum (Fig. 2f) elliptical, rugose in its discal area, punctuated; anterior edge transverse, raised, lateral edges raised as well but to a lesser extent, posterior edge convex. Tegmina (Fig. 2a, b, f) fully developed, coriaceous, densely and regularly punctuated, apex sharply rounded; hind-wings (Fig. 2c, h) slightly infuscated, with a large apical field coiled at rest. Venation as in Fig. 2c, with no clear vein in the apical field. Anal plate symmetrical, concave medially. Subgenital plate small, convex, symmetrical, with two concave indentations where the small and elongate styli attached. Cerci short, stout, monomerous, flatten dorsad but with ventral side bulbous with several setae. Front femurs unarmed, only with a short genual spine, fifth tarsomere as long as the others combined, no pulvillus, claws symmetrical; Hindlegs with first tarsomere almost as long as the others combined, fifth tarsomere longer than the three previous ones, with pretarsal claws symmetrical and lacking pulvilli and arolia.

Genitalia as in Fig. 2d, e. Genitalia of congeneric species have never been illustrated or described.

Measurements Body length (with tegmina): 16 mm; length of tegmina: 13 mm; largest width of tegmina: 4.5 mm; pronotum (width x length): 5.5×2.5 mm.

Diagnosis Differs from *M. magnifica* Shelford (1912) and *M. mimetica* Shelford (1912) in coloration of pronotum and forewings (strongly reddish chestnut in *O. illuminata*) and the color of the hind-wing (mostly translucent in *O. illuminata*). Body coloration as in *Aclavoidea socialis* but more strongly reddened. Pronotum and body wide with stout legs. Strongly differs from *A. socialis* and *M. magnifica* in length of cerci (which are stout and roughly equal with the end of the male's styli). Differs from *A. socialis* in presence of forewing PCu vein. Differs from *Oulopteryx meliponarum* Hebard (1921) in shape of pronotum (nearly circular in *O. meliponarum*), pattern of cross venation between radius and medial vein in hind-wing (roughly parallel in *O. illuminata* but not in *O. meliponarum*), non-setose pronotum, elytra and supra-anal plate (all setose in *O. meliponarum*), and body length larger.

Most similar to *Oulopteryx dascilloides* Hebard (1921) but with the following differences: body coloration reddish chestnut (as opposed to hazel-chestnut in *O. dascilloides*), styli half as long as distance between styli (as opposed to 1/3 the distance in *O. dascilloides*), cerci stouter with less than 1/3 extending past the supra-anal plate (as opposed to nearly half in of cerci extending past plate in *O. dascilloides*), supra-anal plate without setae (setose in *O. dascilloides*) and body length ~15 mm (~8 mm in *O. dascilloides*). Female unknown.

Etymology The specific epithet is from the Latin *illuminatus*, meaning "lighting up or illuminating". It has been chosen because this new species, belonging to the obscure Oulopterygidae family, has shed light on deep convergent evolution in cockroaches.

Discussion

Despite important advances in cockroach molecular systematics with increasing character and taxon sampling (e.g. > 50 genera in Legendre et al., 2015, 2017 and ca. 1 million nucleotides in Evangelista et al., 2019a, b, c), a vast majority of genera—and many more species—have never been included in any formal molecular phylogenetic analysis. We have shortened this gap with sampling of nine genera with unsettled phylogenetic affinities.

Arguably, the most outstanding result is the inference that *Oulopteryx* is sister to Tryonicidae (Fig. 1), since there was no previous finding of them sharing derived features. The biogeographical mismatch among this phylogenetic sister relationship is similarly surprising. This relationship may be between 65 MY [the youngest estimated

age of crown Tryonicidae (Li, 2022)] and 200 MY old [the oldest estimated age of crown Blattidae + Tryonicidae (Li, 2022)], in which case it would be consistent with Gondwanan distribution and vicariance during the Jurassic, or a short dispersal during the Cretaceous.

Behaviorally, this relationship is of great interest, particularly with regard to diet and social behavior. In Blattodea, the prevailing hypothesis tightly links the evolution of eusociality with a xylophagous diet (Legendre & Grandcolas, 2018; Nalepa, 2015). Some Tryonicidae are wood-feeding and solitary (Grandcolas, 1997) while the diet of Oulopterygidae is unknown. *Melyroidea* has been found within excavated logs (Hinkelman et al., 2020), but their diet was not categorized. A recent study on *Melyroidea* in situ reported aggregation, group defensive behavior, and possibly parental care (Hinkelman et al., 2020). Further study is needed to reveal xylophagy or other aspects of social behavior in this and other lineages, exemplifying the desperate need of "natural history" data for numerous taxa (Greene, 2005). Other phylogenetic results are less intriguing but insightful nonetheless. While we did not obtain a robust placement for *Anaplecta* spp., we are able to narrow down possible placements to somewhere within, or sister to, Blattoidea. Recent analyses of mitogenomes (Bourguignon et al., 2018; Li, 2022) have recovered support for *Anaplecta* spp. as sister to *Lamproblatta* sp. Hebard, 1919, but studies have failed to reach congruence over the placement of the latter taxon (Bourguignon et al., 2018; Evangelista et al., 2019a, b, c; Li, 2022). On the other hand, we did find moderate support for *Anaplectoidea* sp. as sister to Blaberoidea *s.s.* This is consistent with Roth (1996)'s finding of genital synapomorphies with Blaberoidea. The genera *Anaplectella* Hanitsch, 1928, and *Malaccina* Hebard, 1929, should be included in future studies to ascertain potential monophyly with *Anaplectoidea* (Roth, 1996) and their position within, or sister to, Blaberoidea *s.s.*

The phylogenetic topology unambiguously suggests the hind-wing apically folded membrane was independently gained nine times and lost at least once (Fig. 1). While multiple acquisitions are strongly supported, the exact number of gains should be taken with caution, as it is influenced by a number of factors. First, the ancestral state reconstruction of the hind-wing apical field uses a very broad definition—any sized apical region of the membrane between the anterior (radial) and anal sectors of the wing. A more restricted definition—an apical expansion of the same membrane that is the apical most point on the wing—would remove the gains leading to *Epilampra* and *Pycnoscelus*. Although most Blattellinae fit the more liberal definition, a number of blattelline genera we included (*Theganopteryx*, *Euhypnorna*, *Hemithrysocera*) fit the more restricted one as well. Another potential source of error is an incomplete sampling of taxa with apically folded hind-wings.

The Pseudophyllodromiidae genera *Chorisoneura*, *Plectoptera* (Rehn, 1951), and *Calhypnorna* (Saussure & Zehntner, 1893) also have apically expanded hind-wings. Phylogenetic studies have included *Chorisoneura* and *Calhypnorna* (Evangelista et al., 2014, 2020), and, while their findings are not entirely congruent, the evidence points to a close relationship with *Macrophyllodromia*—a large-bodied taxon lacking a hind-wing apical field. Other than *Macrophyllodromia*, these taxa were not included in our sample since their genetic data was non-overlapping with our 41 loci. If they were included, it may have resulted in an additional gain within Pseudophyllodromiidae or a deeper placement of the gain seen in *Riatia* sp. Another source of error in the ancestral reconstruction of total hind-wing apical field gains could be from the statistical inference method. The preference for two independent gains in *Anaplectoidea* and Ectobiinae as opposed to on the shorter stem of their ancestor is a feature of the Bayesian inference (Bollback, 2006). An equally parsimonious state reconstruction is a gain of an apical field at the ancestor of *Anaplectoidea* + Blaberoidea *s.s.* and a loss in the ancestor of Pseudophyllodromiidae + Orkrasomeria Evangelista et al. 2020. Finally, we chose to code *Diploptera* as not having apically expanded hind-wings. Although *Diploptera*'s hind-wings are long compared to the fore-wings, their expansion appears to be derived from the anterior section of the wing (Li & Wang, 2015). Coding their apical fields as "present" could have resulted in the inference of at least one additional gain of the apical field. Considering all of the above possible sources of error, the number of possible gains (7–12) and losses (1–3) could differ from our result of 9 and 1, respectively.

Regardless, there is extreme convergence in wing morphology among lineages that diverged deep in evolutionary time—some up to 230 MA (Li, 2022). The biological correlates of this remarkable convergent evolution are unexplored. Cockroach hind-wings are both flight organs (Nalepa et al., 2001) and used in mating rituals (Kotyk & Varadinova, 2017). In other animals, wing size relative to body size is known to affect flight efficacy (e.g., Le Roy et al., 2019; McCulloch & Waters, 2018), but such studies on taxa that are traditionally considered weak fliers are lacking. The interactions between relative wing size, body size (Grabow & Rüppell, 1995), wing membrane thickness, wing resilience (Dirks & Taylor, 2012), and flight capacity (Le Roy et al., 2019; Wootton, 1981) are largely unexplored in Blattodea. In addition to learning about aerodynamic evolution, comparing the folding mechanism of the wing to other organisms with similar apical wing folding, such as beetles or earwigs (Haas, 1999; Kukalova-Peck & Lawrence, 1993), could yield interesting outcomes as well. In fact, many of the cockroaches with expanded hind-wings are considered beetle mimics themselves (Shelford, 1912). Perhaps the morphological constraints of a beetle-like morphology somehow

necessitate hind-wing folding and/or expansion. Exploring these intriguing patterns should be the subject of future studies on the evolutionary drivers of wing evolution.

Declarations

Competing interests The authors declare no competing interests.

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