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Molecular phylogeny and updated classification of jewel damselflies (Odonata: Zygoptera: Chlorocyphidae)

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Abstract

Chlorocyphidae (Odonata: Zygoptera) represent a family of odonates found in tropical Asia and Africa, composed of 162 species. The family is characterized by a pronounced snout-like clypeus, wings that usually extend beyond the abdomen, and striking male coloration correlated with elaborate courtship behavior. Morphological differences between species and among genera are limited. To date, there is no extensive phylogeny of the group. As a result, the current classification is primarily based on coloration and morphological features that have not been tested in a phylogenetic framework. Our taxon sampling includes 90 species (> 55% of diversity). We targeted 92 AHE genes to test previous hypotheses of chlorocyphid classification. We present an updated classification. We recover Chlorocyphidae as monophyletic and *Cyrano* as sister to the remaining genera. We describe two new subfamilies, increasing the number to six: Cyranoinae Fomekong-Lontchi, Kalkman and Bybee **subfam. nov.** and Indocyphinae Fomekong-Lontchi, Kalkman and Bybee **subfam. nov.** A total of 26 species are reclassified to another genus (highlighting the difficulty with Chlorocyphidae morphology and classification), of which 13 are placed in two newly described genera: *Ebenocypha* Fomekong-Lontchi, Kalkman and Bybee **gen. nov.** and *Scapanocypha* Fomekong-Lontchi, Kalkman and Bybee **gen. nov.** Also, the genera *Melanocypha*, *Pachycypha*, *Sclerocypha*, and *Watuwila* are synonymized with *Libellago*. This new classification provides a framework for future studies of chlorocyphid evolution, including their courtship and biogeography.

Keywords

anchored hybrid enrichment, Cyranoinae, *Ebenocypha*, *Scapanocypha*, Indocyphinae

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1. Introduction

Chlorocyphidae, commonly known as "jewels," are characterized by a snout-like clypeus, a short thick body, and long, narrow wings exhibiting a wide range of coloration, often including iridescence (Fig. 1). They occur in the tropical parts of Africa and Asia, and 162 species are currently recognized and placed in 19 genera (Paulson et al. 2025), with no genera shared between the two continents. With 15 genera and 112 species, the Asian fauna is more diverse than that of Africa where four genera and 50 spe-

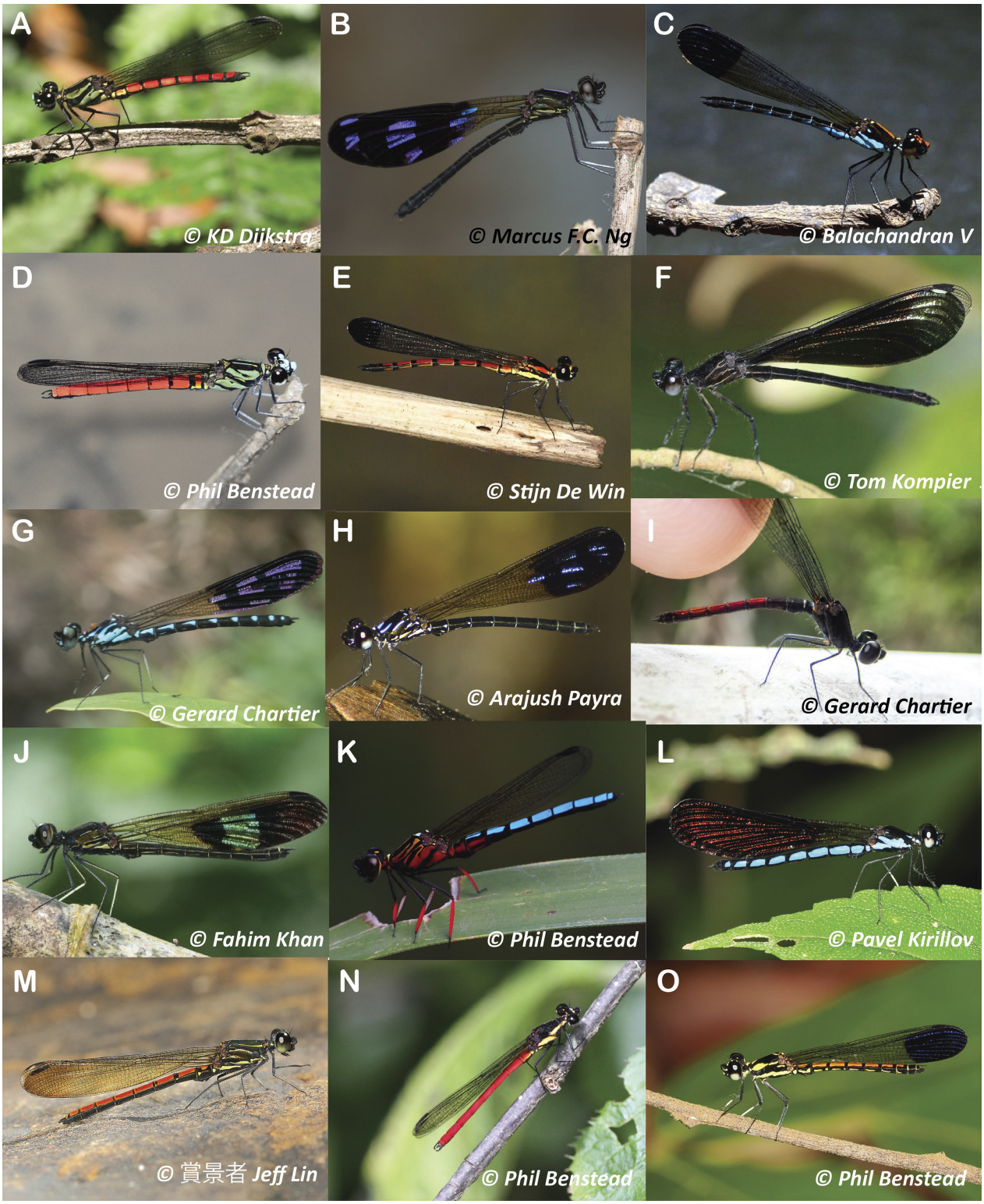


Figure 1. Some representatives of Chlorocyphidae: **A** *Africocypha centripunctata*; **B** *Aristocypha fenestrella*; **C** *Calocypha laidlawi*; **D** *Chlorocypha trifaria*; **E** *Disparocypha biedermanni*; **F** *Ebenocypha orea*; **G** *Heliocypha perforata*; **H** *Heterocypha vitrinella*; **I** *Libellago hyalina*; **J** *Paracypha unimaculata*; **K** *Platycypha caligata*; **L** *Rhinocypha frontalis*; **M** *Scapanocypha taiwana*; **N** *Stenocypha jacksoni*; **O** *Sundacypha petiolata*.

cies occur. The most diverse genus, *Rhinocypha* Rambur, 1842, is from Asia, represented by 42 species.

Males of most species of Chlorocyphidae are very colorful, having yellow, blue or red patterns on the body. In addition, in Asia a majority of species have partially pigmented wings, sometimes with patches of iridescence. These wing markings vary from simple dark tips (e.g. *Libellago* Selys, 1840) to covering most of the wing (e.g. *Rhinocypha monochroa* Selys, 1873). All African species have transparent wings, lacking wing pigmentation. They do, however, tend to be more colorful on the abdomen and legs (Pinhey 1967) with some species of *Platycypha* Fraser, 1949 even having expanded tibiae that are bright white on the inner side and red on the outside.

Chlorocyphidae is recognized as monophyletic (Bybee et al. 2021; Newton et al. 2026) with solid synapomorphies including the expanded clypeus, abdomen shorter than the wings (except in *Rhinoneura* Laidlaw, 1915), and nymphs having a reduced epiproct and spike-like paraprocts (Orr et al. 2024). Recent phylogenetic efforts based on reduced genome data (e.g., anchored hybrid enrichment [AHE] and transcriptomes) have recovered Calopterygidae as sister group to Chlorocyphidae with varying support (Bybee et al. 2021; Kohli et al. 2021; Suvorov et al. 2022; Carter et al. 2026). The sister group relationship is supported across most phylogenetic analyses, with varying support, likely due to high introgression across Calopterygoidea and limited taxon sampling across the group (Bybee et al. 2021; Suvorov et al. 2022). Previous Sanger-based molecular hypotheses using 5.8S, 12S, 16S, 18S, 28S, COI, COII, H3, ITS1 and ITS2, have placed other families as sister group to Chlorocyphidae, notably Devadattidae (Bybee et al. 2008; Dijkstra et al. 2014), Protolestidae (Dijkstra et al. 2014), and Euphaeidae (Dumont et al. 2005). A morphological and molecular analysis did recover Chlorocyphidae as sister to a portion of Calopterygoidea (Bybee et al. 2008).

Based on Sanger sequencing of three genes, Dijkstra et al. (2014) proposed to divide Chlorocyphidae into four groups, but refrained from officially naming these: 'Chlorocyphinae', 'Disparocyphinae', 'Libellagininae', and 'Rhinocyphinae'. The validity of these groups still needs to be tested with a wider taxon sampling and a more extensive set of genes. Intrafamilial relationships have not been tested, especially in Rhinocyphinae, which Dijkstra et al. (2014) found as non-monophyletic. Moreover, revisions are likely necessary to form stable taxonomic groups for some genera like *Aristocypha* Laidlaw, 1950, *Libellago* and *Rhinocypha* (Dijkstra et al. 2014).

While the species and genera within the family Chlorocyphidae show a wide array of differences in color and pattern of the body and wings, the differences in morphology are generally limited (van Tol 2007). Morphological characters that are useful for genus recognition in most odonates families, such as the shape of the male's anal appendages or secondary genitalia, are largely similar between the genera of Chlorocyphidae. Chlorocyphid genera have mostly been distinguished based on wing venation (Fraser 1949; van Tol 2007; van Tol and Günther 2018), an exception being the genus *Rhinoneura*, which is characterized by an abdomen longer than the wings.

Differentiation between species is mainly based on body coloration (van Tol and Günther 2018). Similar to chlorocyphid genera, studies of the secondary genitalia and anal appendages did not result in characters of value for classification or identification of chlorocyphids (Cowley 1937; Pinhey 1967; van Tol and Günther 2018). Females lack the bright colors of the males and therefore species identification mostly relies on males. However, the use of geometric morphometrics and Field Emission Scanning Electron Microscope (FESEM) have shown morphological differences between females of three sympatric species (*Aristocypha fenestrella* (Rambur, 1842), *Heliocypha biforata* (Selys, 1859), *Heliocypha perforata* (Percheron in Guérin-Méneville and Percheron, 1835)), notably in the size of the articulated setae, the distribution of the basiconic sensilla, the carina of the sheathing valves, and the distribution and size of the sensilla on the tip of the stylus (Mamat et al. 2021). These approaches could potentially lead to the inclusion of more females in taxonomic works on Chlorocyphidae in the future.

Currently, there is no phylogeny focused on Chlorocyphidae. Dijkstra et al. (2014) provided the most extensive phylogeny of Chlorocyphidae to date, with 24 species representing ~15% of the diversity for the family. We aim to: 1) produce the first higher-level phylogeny for the family, 2) test the monophyly of the genera, and 3) address taxonomic issues at the genus level that may arise based on our phylogenetic hypothesis.

2. Material and methods

2.1. Taxon sampling

Sixteen of the 19 genera (~84%), 90 species (~56%) (a total of 105 taxa including outgroup taxa) were included in our phylogeny. All unsampled genera are monotypic (*Calocypha* Fraser, 1949, *Heterocypha* Laidlaw, 1950 and *Sclerocypha* Fraser, 1949) and representatives of each could not be obtained for DNA extraction. For each genus we sampled, the number of species included vs. the total diversity is presented in Table 1.

The specimens for this project were obtained from the Florida State Collection of Arthropods (Gainesville, Florida), the insect cryo-collection of the Monte L. Bean museum at Brigham Young University (BYU, Provo, UT), the American National History Museum (AMNH, New York City, NY), and the Naturalis Biodiversity Center (Leiden, The Netherlands). Old pinned dry and wet specimens were utilized in this project as they have been shown to be useful in studies using anchored hybrid enrichment (Goodman et al. 2023).

Fifteen species from eleven Calopterygoidea families (according to Bybee et al. 2021) were included as outgroup taxa: Argiolestidae, Calopterygidae, Devadattidae, Dicteriadidae, Heteragrionidae, Lestoideidae, Platystic-

Table 1. Diversity of species included in the topology; columns: number of species sampled (nss), number of species reported (nsr), percentage of species sampled (pss in %).

Genus	Number of species sampled	Number of species reported	Percentage of species sampled (%)
Africocypha	1	2	50
Aristocypha	6	11	54.55
Calocypha	0	1	00
Chlorocypha	11	29	37.93
Cyrano	2	2	100
Disparocypha	1	1	100
Ebenocypha **gen. nov.**	6	9	66.67
Heliocypha	8	11	72.73
Heterocypha	0	1	00
Indocypha	4	7	57.14
Libellago	19	29	65.52
Paracypha	1	1	100
Platycypha	9	14	64.29
Rhinocypha	12	31	38.71
Scapanocypha **gen. nov.**	4	6	66.67
Stenocypha	3	5	60
Sundacypha	2	2	100

tidae, Polythoridae, Pseudolestidae, Rhipidolestidae and Thaumatoneuridae.

2.2. DNA extraction

One leg (preferably metathoracic, including a small chunk of flight muscle) was removed from specimens using sterilized forceps and placed in a 2 mL Eppendorf vial. The DNA was then isolated using the Qiagen DNeasy Blood & Tissue Kit, following the recommendations of the manufacturer with some adjustments notably a longer incubation in proteinase K (48 hours), and a higher volume of the elution buffer (30 µl). The DNA was later quantified using a Qubit 4 fluorometer with the High Sensitivity DNA assay.

2.3. Targeted Capture and DNA sequencing

Anchored hybrid enrichment (Lemmon et al. 2012) and DNA sequencing were performed by Rapid Genomics LLC (Gainesville, Florida). The captured probes were a subset of 500 probes previously described in Bybee et al. (2021) and used in Goodman et al. (2023). The final probe set targeted only 92 genes (90 nuclear and 2 mitochondrial) (representing > 20,000 bp) in order to prioritize a broader taxon sampling.

2.4. Cleaning and organizing of molecular data

Raw sequences were trimmed off adapters using *fastp* (Chen 2023). The trimmed reads were then assembled using the targeted iterative baited assembly method described in Breinholt et al. (2018) with the probe sequences as references and SPAdes as the assembler (Bankevich et al. 2012; Breinholt et al. 2018). We assessed orthology by using BLAST to query each assembled sequence against the *Tanypteryx hageni* (Selys, 1879) reference genome (Tolman et al. 2023). We removed sequences with hits to multiple contigs when a secondary hit generated a bit score > 90% of the primary hit. We then identified contaminant DNA with an all-by-all -BLAST search using the UBLAST feature of the USEARCH suite (Edgar 2010). We then removed hits that were identical across >98% of the assembled sequence that belonged to different families or genera.

Only the probes region was targeted in this project. Assembled loci were aligned using MAFFT v7.520 (Katoh and Standley 2013). To remove ambiguously aligned positions from the multiple sequence alignment of each locus, we used Aliscore v2.0 and Alicut v2.31 using the default parameters (Kück et al. 2010; Misof and Misof 2009). Samples that were consistently recovered among the outgroup taxa in preliminary phylogenetic analyses, despite their expected placement within the ingroup were removed from further analyses (*Africocypha centripunctata* (Gambles, 1975), *Aristocypha trifasciata* (Selys, 1853), *Chlorocypha wittei* Fraser, 1955, *Libellago corbeti* van der Poorten, 2009, *Libellago naias* Lieftinck, 1932, *Libellago orri* Dow and Hämäläinen, 2008, *Platycypha pinheyi* Fraser, 1950, *Rhinocypha huai* (Zhou and Zhou, 2006), *Rhinoneura caerulea* Kimmins, 1936).

2.5. Maximum Likelihood tree reconstruction

Trees were reconstructed using Maximum Likelihood in IQ-TREE2. Each locus was treated as a separate partition. To optimize computation, partition merging was automat-

ically performed using the command -m MFP+MERGE, which merges similar partitions based on the Bayesian Information Criterion (BIC). The best-fit model for each resulting merged partition was selected using ModelFinder (Kalyaanamoorthy et al. 2017) integrated in IQ-TREE2 (Minh et al. 2020). An ultrafast bootstrap with 1,000 replicates and branch length optimization was performed to assess the node support values on the tree. The final tree was visualized with FigTree v1.4.4 (Rambaut 2018).

2.6. Quartet sampling

In order to provide another insight to nodal support in the maximum-likelihood topology, we used the quartet sampling framework from Pease et al. (2018). This approach assesses support by repeatedly sampling four-taxon subsets and comparing the likelihoods of all the possible quartets topologies. Three nodal scores are calculated: Quartet Concordance (QC) measures to what extent the three possible quartets favor the topology shown in the tree; Quartet Differential (QD) which determines whether the two discordant quartets occur at similar or unequal frequencies; and Quartet Informativeness (QI) which estimates the proportion of sampled quartets that contain enough phylogenetic information to distinguish among alternative resolutions. We also used Quartet Fidelity (QF) to evaluate terminal nodes behavior. Quartet likelihoods were estimated using IQ-TREE2 from the concatenated alignment and the inferred maximum-likelihood tree, with 100 quartet replicates sampled per focal branch.

3. Results

3.1. AHE results

The total number of recovered loci varied from 7 (*Melanocypha snellemanni* (Albarda in Selys, 1879)) to 92, with an average of ~86 and a median of 85.62 loci per species. The loci lengths varied between 121 and 4653 bp for an average of ~336 bp; they contained an average of ~83 parsimony informative characters (13–465), resulting in a dataset of 7,730 parsimony-informative sites and a combined aligned matrix length of 30,656 bp.

3.2. Phylogenetic results

Chlorocyphidae was recovered as monophyletic with Calopterygidae as the sister group. We recovered six main lineages within Chlorocyphidae, with high support (Fig. 2). The genus *Cyrano* was sister to all other species of Chlorocyphidae. Several genera were not recovered as monophyletic (e.g., *Rhinocypha*) and others were placed within existing genera (e.g., *Rhinoneura*). We provide a brief synopsis of taxonomic results for each clade below.

Cyranoinae **subfam. nov.** (Clade 1): This clade includes both species of *Cyrano* and has a bootstrap support (= bs) of 100%. *Cyrano* is sister to the rest of Chlorocyphidae with 100% bs.

Chlorocyphinae (Clade 2): This clade includes all species from the African continent. *Stenocypha* is sister to the rest of the African genera, i.e. to the clade *Platycypha* + *Africocypha* + *Chlorocypha*. Clade 2 and *Stenocypha* have 100% bs; both *Platycypha* and *Chlorocypha* have < 80% bs; *Africocypha* and *Chlorocypha* were recovered as non-monophyletic (for details see Fig. 2).

Indocyphinae **subfam. nov.** (Clade 3): Four of the seven species of *Indocypha* form a fully supported monophyletic group. *Indocypha* is sister to all other Asian species except those placed in the genus *Cyrano*.

Disparocyphinae (Clade 4): *Disparocypha biedermanni* is the sole member of clade 4. It is sister to clade 5 + 6 (98% bs).

Libellagininae (Clade 5): This clade contains all members of *Libellago*, but that genus is not monophyletic due to the recovery of the monotypic genera *Pachycypha*, *Melanocypha* and *Watuwila* as subordinate in *Libellago*. Four main lineages appear within clade 5. Overall, the support for clade 5 and its subclades is relatively low.

Rhinocyphinae (Clade 6): This clade is composed of four subclades. The subclade 6.1 is composed of the *Sundacypha* species and is sister to the subclade 6.2, which is made up mostly of *Rhinocypha* species (including the type species, *Rhinocypha tincta*). *Rhinoneura* is embedded within *Rhinocypha*, rendering it non-monophyletic. Overall support for the clade and these two subclades is high. The subclades 6.3 and 6.4 are the most complex of the phylogeny, with *Rhinocypha*, *Aristocypha* and *Heliocypha* recovered as non-monophyletic. The subclade 6.3 includes further members of the non-monophyletic genus *Rhinocypha*. The subclade 6.4 contains *Rhinocypha unimaculata* as sister to *Heliocypha* + *Aristocypha*, and *Aristocypha iridea* as sister to *Heliocypha*. The support in those two subclades is variable.

4. Discussion

Our results represent the most comprehensive phylogeny of Chlorocyphidae, representing 55% of the species diversity of the group. Our results align with previous phylogenetic hypotheses of Zygoptera based on morphological and molecular data, which recovered Chlorocyphidae as monophyletic (Bybee et al. 2021, 2008; Dijkstra et al. 2014; Dumont et al. 2010, 2005; Kohli et al. 2021; Rehn 2003; Suvorov et al. 2022). Van Tol (1998) utilized 11 morphological characters coded from the wings to establish phylogenetic relationships among the genera found in Southeast Asia. Our result for the generic relationships does not recover the relationships inferred by van Tol (1998). In our results, several genera were recovered as non-monophyletic (*Africocypha* Pinhey, 1961, *Aristocypha* Laidlaw, 1950, *Chlorocypha* Fraser, 1928,

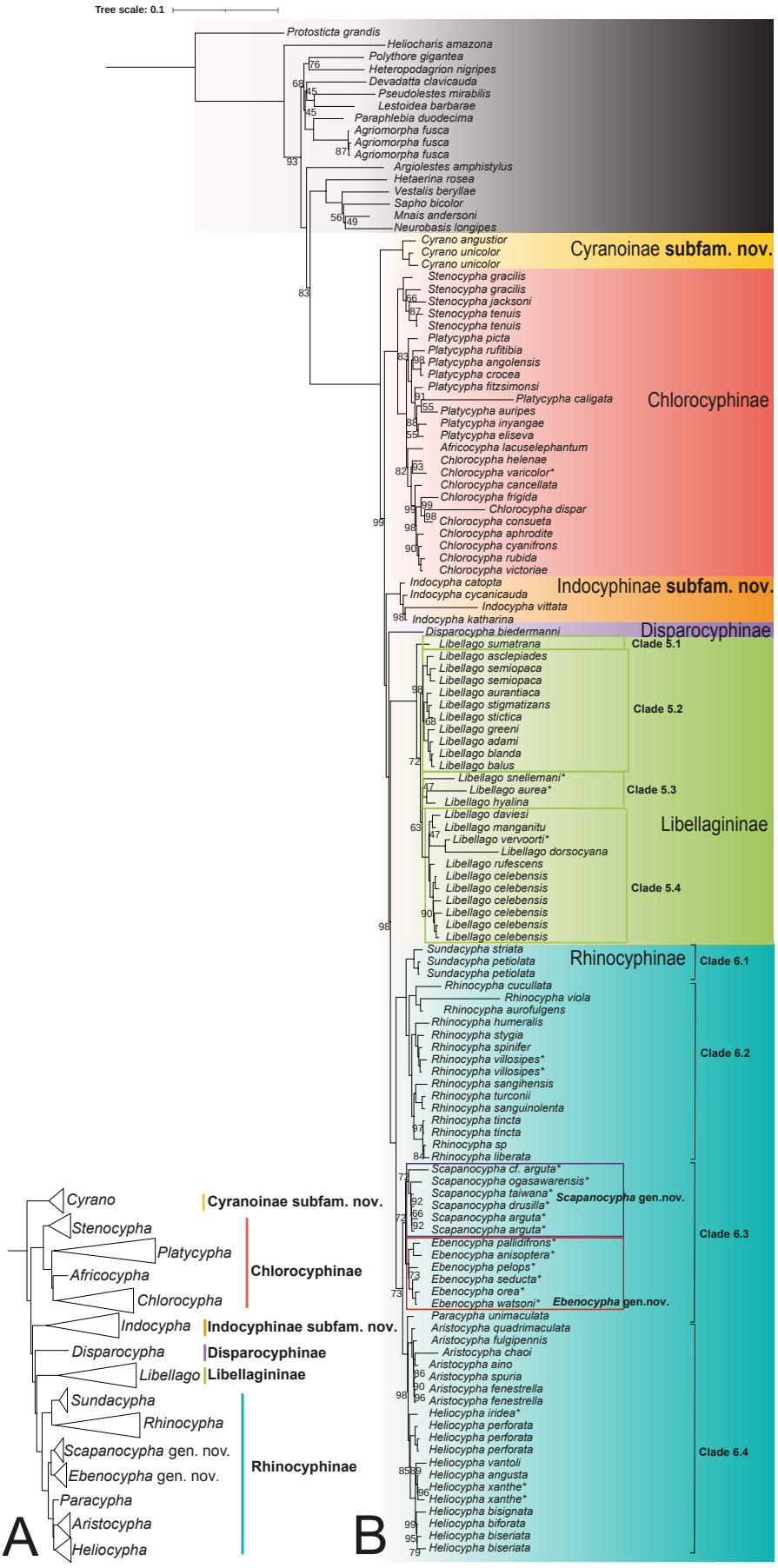


Figure 2. Phylogenetic relationships of Chlorocyphidae based on 20 kbp (92 loci) of molecular data generated from anchored hybrid enrichment. The topology was obtained through ML recovered from IQTREE. Nodal support is Ultra-Fast bootstrap approximation. Only support values < 100 are shown. **A** Genus level relationships; **B** Species level relationships. Across the topology, * represents updates from the previous classification scheme for the family, ** reflects a subfamily update.

Heliocypha Fraser, 1949, *Libellago* Selys, 1840, *Platycypha* Fraser, 1949, *Rhinocypha* Rambur, 1842), which makes it difficult to define the intergeneric relationships and study the evolution of Chlorocyphidae. We address the classification of each subfamily below following our phylogenetic result (Fig. 2).

Cyranoinae Fomekong-Lontchi, **Kalkman and Bybee subfam. nov. (Clade 1).** Our phylogeny recovered *Cyrano* as sister to all Chlorocyphidae, unlike previous classifications. For instance, Dijkstra et al. (2014) placed *Cyrano* as sister to all Asian species (ML reconstruction with 16S + 28S) or sister to all Chlorocyphidae excluding *Sundacypha* Laidlaw 1950 and *Rhinoneura* (Bayesian reconstruction with 16S + 28S + COI). *Cyrano* and *Indocypha* were previously hypothesized to be the earliest "unspecialized grade" within *Rhinocypha* (Laidlaw 1950); but our reconstruction depicts both *Cyrano* and *Indocypha* to be distinct lineages amongst Chlorocyphidae, and differ from other Asian lineages. Therefore, we describe the subfamily Cyranoinae **subfam. nov.** to accommodate the genus *Cyrano*.

Chlorocyphinae (Clade 2). This clade includes all species found on the African continent. The subfamily "Chlorocyphinae" was previously proposed by Dijkstra et al. (2014) when they recovered African species as monophyletic. They are split up into four genera: *Africocypha* Pinhey, 1961, *Chlorocypha* Fraser, 1928, *Platycypha* Fraser, 1949 and *Stenocypha* Dijkstra, 2013. In *Chlorocypha*, Dijkstra (2003) mentioned taxonomic issues caused by the variability of male coloration. This has resulted in the descriptions of several species that were later synonymized. Beyond color, morphological characters that delineate species are lacking (Dijkstra 2003). Pinhey (1967) has divided *Chlorocypha* into groups based on the general coloration of the abdomen, the markings in the thorax, the extent of black markings, but these groups are still to be tested in a phylogenetic context. Dijkstra (2013) split *Chlorocypha* into two genera based on differences in the relative abdominal diameter of species, resulting in the genus *Stenocypha* whose members have a thinner abdomen.

Here *Stenocypha* was recovered as sister to the African genera, in line with Dijkstra et al. (2014). However, in contrast to the current classification, *Stenocypha* and *Platycypha* were recovered as monophyletic in our analyses. We have now organized the species between the African genera to be now monophyletic.

Africocypha lacuselephantum and *A. centripunctata* were recovered as sister species by Dijkstra et al. (2014), but *A. centripunctata* was excluded from our final taxon sampling because of poor sequence quality. In our analyses, *A. varicolor* was not recovered as sister to *A. lacuselephantum*, but instead within *Chlorocypha*, as sister to *C. helenae*. *Africocypha varicolor* and *C. helenae* both possess two distinct abdominal colors. However, this character cannot be considered as a synapomorphy for the clade because it also occurs in *C. cancellata* and *C. curta*, which are recovered in other clades in our phylogeny. The placement of *A. varicolor* within *Chlorocypha* is unexpected. In fact, *A. varicolor* was initially placed in *Africocypha* by Dijkstra et al. (2015) because it shares many morphological features with *A. lacuselephantum* and *A. centripunctata*, notably the dorsally black S9 and S10; the paraprocts at least half as long as the cerci, the completely black legs, the labrum, anteclypeus and genae that are entirely blue (Dijkstra et al. 2015; Dijkstra 2017; Pinhey 1961a). However, despite these morphological differences, the quartet-sampling more consistently supports the placement of *A. varicolor* as sister to *C. helenae* with 57 counts over the two alternative placements (*Chlorocypha aphrodite*, *Africocypha varicolor*) and (*Africocypha varicolor*, *Neurobasis longipes*) that were sampled 27 and 6 times respectively (Files S1–S3). Nevertheless, we acknowledge that with this moderate support, additional samplings, including particularly *A. centripunctata* are necessary to test this relationship. For now, maintaining *A. varicolor* in *Africocypha* will render the genus non-monophyletic. We therefore reclassify *A. varicolor* as *Chlorocypha varicolor* **comb. nov.**

Regarding the relationships amongst the "blue *Platycypha*" (*P. angolensis*, *P. bamptoni*, *P. crocea* and *P. rubriventris*), a radiation originating from Angola (Kipping et al. 2017), our tree supports the recent transfer of blue Angolan species from *Chlorocypha* to *Platycypha* by Kipping et al. (2017), as only *P. angolensis* and *P. crocea* were recovered as sister species.

Indocyphinae Fomekong-Lontchi, **Kalkman and Bybee subfam. nov. (Clade 3).** This clade includes representatives of the genus *Indocypha*, which we reclassify in a new subfamily Indocyphinae **subfam. nov.** *Indocypha* is divided into two groups based on the size of the wings relative to the abdomen (Hämäläinen 2014). One group is represented by *Indocypha svenhedini* and *I. catopta* where the wings are distinctively longer than the abdomen and anal appendages combined; and the second group is composed of the remaining species, where the wings are slightly longer than the abdomen (not more than 1 mm) (Hämäläinen 2014). Our tree tends to support that separation as *I. catopta* is sister to the rest of the species. However, a larger taxon sampling including all the species known in the genus is necessary to test if that character can function as a synapomorphy for the two main clades of *Indocypha*.

Disparocyphinae (Clade 4). *Disparocypha biedermanni* was recovered as a monotypic sister lineage to the remaining Asian Chlorocyphidae genera. The placement of this monospecific genus has been contentious for some time (Günther 2020; van Tol 2007, 1998; van Tol and Günther, 2018). Van Tol (1998) hypothesized that it is a recently diverged lineage due to the reduction of the veins Cu1 and Cu2. A molecular estimate of the age of diversification from the rest of the Chlorocyphidae will address this hypothesis. However, from our current phylogeny it seems unlikely that this is a recently diverged lineage, as it is basal to two of the larger subfamilies. Based on its reduced Cu1 and Cu2, *D. biedermanni* was placed in its

own subfamily, Disparocyphinae (Munz 1919), which we find support for in our molecular phylogeny. The courtship behavior of *D. biedermanni* appears to be simple and unspecialized, which is unusual in Chlorocyphidae (Günther 2008). A non-structured courtship has also been reported in *Libellago hyalina*, *L. celebensis* and *L. rufescens* (Günther 2020). Due to the dearth of information on courtship behavior, it is still unknown how that character evolved across chlorocyphids.

Libellagininae (Clade 5). The subfamily was proposed by Laidlaw (1920), and Fraser (1949) suggested that *Libellago* is potentially placed at "the base of the family Chlorocyphidae." However, in our analyses, the subfamily Libellagininae is not the sister-group of the rest of Chlorocyphidae.

Libellagininae is divided into four main lineages with *Libellago sumatrana* as sister to all *Libellago*. Our topology shows that the genera *Melanocypha*, *Pachycypha* and *Watuwila* are nested within *Libellago*. These genera are characterized by the sectors originating from the arculus all starting at the same point (van Tol 1998). As a result, they are synonymised with *Libellago*. Van Tol and Günther (2018) hypothesized that *Watuwila* was related to *Libellago*. In a reconstruction of fourteen chlorocyphid genera (thirteen from Southeast Asia and *Chlorocypha*) based on eleven morphological characters from wing venation, *Melanocypha* was recovered as equally related to *Libellago* + *Pachycypha* (van Tol 1998). Our reconstruction confirms that *Pachycypha*, as well as *Watuwila* and *Melanocypha* are well supported members of *Libellago*.

While *Sclerocypha* was not included in our study, van Tol (1998) recovered that genus as sister to *Melanocypha* + (*Libellago* + *Pachycypha)*. Also, Dijkstra et al. (2014) found that *Sclerocypha bisignata* and *Pachycypha aurea* were embedded in a clade of *Libellago*. Following the evidence from both van Tol (1998) and Dijkstra et al. (2014) along with our results, we therefore reclassify *Sclerocypha* into *Libellago*.

Historically, the differentiation between the clades of *Libellago* was based on morphological characters. Dijkstra et al. (2014) recovered two subclades within Libellagininae and hypothesized that the two were differentiated by the presence/absence of dark markings on the tips of the wings. The character of dark markings at the wing tips that supported Dijkstra et al.'s (2014) hypothesis was not recovered in our analysis, as both clades contain species with dark-tipped wings. Of note, in our analysis two species with clear wings are sister species: *Pachycypha aurea* and *Libellago hyalina*. Orr et al. (2024), based on the COI gene, recovered a clade that included *Pachycypha aurea*, *Libellago hyalina*, and *Libellago orri*. The sister relationship between *Libellago orri* and *Libellago hyalina* was previously hypothesized by Dow and Hämäläinen (2008) due to the similarities of some body markings between the two, the only differences being the relative size, with *L. orri* being smaller; and the coloration of the male abdomen, where *L. orri* lacks any metallic areas and red coloration on the dark abdomen. Adding *L. orri* in future reconstructions will help to test this relationship. A neighbor-joining reconstruction by Orr et al. (2024) based on COI, could not separate *L. hyalina* or *L. orri* as each of them did not form distinct monophyletic clades; the past geographic isolation is hypothesized to be the sole driver of speciation for the two species. Also, it was suggested that the structure of the flattened anterior facet (situated between the anteclypeus and the postclypeus) could be used to identify closely related species in *Libellago* (Hämäläinen 2002). In fact, three states are recognized: a) absent, b) flat, and c) intermediary between flat and absent. But in our case, none of these states represent a diagnosable character for either of the subclades.

A biogeographic pattern seems to emerge as a differentiation criterion between the clades in *Libellago*. All species of subclade 5.3, except for *Libellago dorsocyana* (known from Kalimantan) (Fig. 2) are endemic to Sulawesi, while the species of subclade 5.2 are not reported from Sulawesi, except for *L. asclepiades* which is endemic to Sulawesi. An ancestral area reconstruction will help to determine how the species in this genus dispersed across Southeast Asia and specifically in the islands of Sulawesi. *Libellago celebensis* presents several forms currently considered as subspecies that are parapatric in their distribution, and each is limited to a specific area of the island (van Tol 2007). Further investigations are necessary to address their actual status (van Tol 1998).

The only *Libellago* endemic to Sulawesi (*L. xanthocyana*) is not included in our work, but we expect it to fall into subclade 5.2 (Fig. 2). According to van Tol. (2007), the markings on the abdomen are close to the ones observed in *L. asclepiades*. The two species are differentiated by the color and pattern of the abdomen. The two may be sister species, but the hypothesis is yet to be tested.

Rhinocyphinae (Clade 6). Previous phylogenetic reconstructions placed *Sundacypha* as sister to *Rhinocypha tincta* + (*Rhinocypha spinifer* + *Rhinoneura caerulea*) or *Rhinocypha tincta* + *Rhinoneura caerulea* (Dijkstra et al. 2014). Our reconstruction recovered *Sundacypha* as sister to one of the clades in a non-monophyletic assemblage of *Rhinocypha*.

The non-monophyly of *Rhinocypha* aligns with previous studies that proposed it should be split (Dijkstra et al. 2014; van Tol 1998; Zhang 2019). In Dijkstra et al. (2014), *Rhinocypha* formed two clades, one largely composed of continental species and the second composed of entirely insular species. We found the same pattern among the clades we recovered. The characters traditionally used to distinguish *Rhinocypha* species are based on the coloration patterns on the head, the thorax, and the abdomen (van Tol and Günther 2018), but more recently, the coloration and the reflective patterns on the wings have also been considered (Günther 2008, 2001; van Tol and Günther 2018). We propose two new genera within Rhinocyphinae (*Scapanocypha* **gen. nov.** and *Ebenocypha* **gen. nov.**) supported by synapomorphies. *Rhinocypha aurofulgens*, *R. cucullata* and *R. viola* form a natural grouping Orr (2002) that was recovered in our tree, but as opposed to the hypothesis of Orr (2002) where *R. viola* was sister to the two others, our hypothesis sup-

ports *R. cucullata* as sister to *R. viola* and *R. aurofulgens*. This clade is characterized by the presence of a subapical flange on S2 of the male (Orr 2002).

From the group *R. sanguinolenta*/*dorsosanguinea*/*turconii* (limited to the Philippines) defined by van Tol and Rozendaal (1995) based on morphological similarities, we did not include *R. dorsosanguinea*. The two other species were, however, strongly supported as sisters.

We recovered *Rhinoneura villosipes* as sister to *Rhinocypha spinifer*, like Dijkstra et al. (2014). The two species in the genus *Rhinoneura* and *Rhinocypha spinifer* share distinctive cerci with the apical part turned sharply downward (Rory Dow pers. comm.). Orr et al. (2024) recovered the two species of *Rhinoneura* embedded in *Rhinocypha* based on COI data. The wing venation of *Rhinoneura* and *Rhinocypha* is similar, which led Laidlaw (1915) to hypothesize that it is related to *Rhinocypha*. However, the slender and long abdomen, the petiolate and long wings, the large and inflated pterostigma, and the characteristic anal appendages were enough morphological evidence to describe it as a separate genus by Laidlaw (1915). Although morphologically distinct, the molecular data place *Rhinoneura* as a member of *Rhinocypha*. Our reconstruction recovers two specimens of *Rhinoneura villosipes* as *Rhinocypha*. We hypothesize that *Rhinoneura caerulea* is a member of *Rhinocypha*, although not included in this study.

Van Tol and Günther (2018) recovered the clade of *Rhinocypha* from Sulawesi, to be sister to *R. tincta* + *R. colorata*. This relationship was previously hypothesized by van Tol (2007). The *Rhinocypha tincta* group is defined to include *Rhinocypha colorata*, *R. flavipoda*, *R. frontalis*, *R. hageni*, *R. humeralis*, *R. monochroa*, *R. pelengensis*, *R. phantasma*, *R. sangihensis*, *R. tincta*, *R. togeanensis*, and *R. virgulata* (van Tol and Günther 2018). The distribution extends West to East, from the Philippines to New Britain (Papua New Guinea) and the Solomon Islands (van Tol and Gassmann 2007). The group remains a challenging group due to morphology and subspecies proliferation (van Tol and Günther 2018). Of all *Rhinocypha* reported from Sulawesi, only *R. sangihensis* is included in our phylogeny. We found *R. sangihensis* and *R. tincta* in two separate but sister clades. Our phylogeny failed to provide enough taxon sampling to address relationships between the species in the *Rhinocypha tincta* group. Future investigations should address this issue to better define their classification and potentially their diversification; and also include all subspecies of *R. tincta* (*tincta tincta* Rambur, 1842, *tincta adusta* Lieftinck, 1949, *tincta amanda* Lieftinck, 1938, *tincta dentiplaga* Lieftinck, 1938, *tincta retrograda* Lieftinck, 1938, *tincta sagitta* Lieftinck, 1938, *tincta semitincta* Selys, 1869) and *R. frontalis* (*R. frontalis frontalis* Selys, 1873 and *R. frontalis sulselensis* van Tol and Günther, 2018) to determine their validity. For instance, van Tol and Günther (2018) found that the genetic distance between populations of *R. frontalis* was greater than between two closely related species, *R. monochroa* and *R. phantasma.* This shows that a lot of research still has to be done in this group.

We describe two new genera to address the non-monophyly of *Rhinocypha*. The genus *Scapanocypha* Fomekong-Lontchi, Kalkman and Bybee **gen. nov.** represents all the species previously known from the *Rhinocypha drusilla*-group, which was proposed and extensively described by Wang et al. (2013). *Rhinocypha* cf. *arguta* was recovered as a sister to the rest of species in *Rhinocypha drusilla* group. Wang et al. (2013) made a similar observation based on the mitochondrial gene COI. The sister relationship between *R. drusilla* and *R. arguta* was also recovered in our study. *Rhinocypha watsoni* was hypothesized by van Tol and Rozendaal (1995) to be closely related to *Rhinocypha drusilla*, but our study recovered them as belonging to two different genera. The discoloration following the preservation of specimens in ethanol probably misled the hypothesis of relationship between *R. watsoni* and *R. drusilla* (Hämäläinen and Divasiri 1997; Wilson and Reels 2003). *Rhinocypha watsoni* instead is to be reclassified in the second new genus, *Ebenocypha* Fomekong-Lontchi, Kalkman and Bybee **gen. nov.**

Ebenocypha represents the Rhinocyphinae that have a largely black abdomen and hindwing being broader than the forewing. *Rhinocypha ignipennis*, *R. selysi*, *R. trimaculata* and *R. heterostigma* were not sampled in our study; however, due to morphological similarity, we move them to *Ebenocypha*. Their exact placement in the genus *Ebenocypha* is not certain, and they are suspected to be synonyms with each other. For example, the main difference between *Rhinocypha ignipennis* and *R. trimaculata* is that *R. ignipennis* is larger and lives at higher altitudes (Khan and Hämäläinen 2021). Also, *Rhinocypha peitho* is morphologically close to *R. pelops* (Hämäläinen 2017) but with the absence of *R. peitho* from our taxon sampling, further investigations are necessary to test that relationship at the molecular level. In fact, the species seems to be known only from the holotype, but we propose reclassifying *R. peitho* in the genus *Ebenocypha* **gen. nov.** due to the morphological similarities with other species reclassified in that genus. *Rhinocypha ignipennis* and *R. trimaculata* are morphologically similar, but in *R. trimaculata*, the transverse transparent wingspots are shorter (Selys 1879). The cells covered by the transparent wingspots in the hindwings are also different between the two species. In females, the hindwings are darker and burnt brown in *R. trimaculata* as opposed to more hyaline and greenish yellow in *R. ignipennis* (Khan and Hämäläinen 2021).

Some authors like Babu (2014) have persisted in using *Rhinocypha unimaculata* in recent years, while others have used *Paracypha unimaculata* (Kalkman et al. 2020). Our analysis confirms that the genus *Paracypha* described by Fraser (1949) is valid and should be used. *Paracypha unimaculata* differs from other genera by the presence of "two rows of cells between the anal vein and the margin of the wing" (Fraser 1949). The species is relatively large compared to other members of the family, with a hindwing length of 27–30 mm (Fraser 1949; Selys-Longchamps 1853). *Paracypha* was recovered as sister to all *Aristocypha* + *Heliocypha* with high support.

Heliocypha and *Aristocypha* have sometimes been treated as subgenera of *Rhinocypha* (Dijkstra et al. 2014;

van Tol and Günther 2018) but based on our results, this would require all genera in Rhinocyphinae to be reclassified as subgenera of *Rhinocypha*.

We recovered *Aristocypha iridea* as sister to *Heliocypha*. This relationship has already been hypothesized by Laidlaw (1950) as the wing coloration pattern in *A. iridea* resembles the general pattern observed in *Heliocypha*. Thus, we reclassify *Aristocypha iridea* as *Heliocypha iridea*. Dow et al. (2024) hypothesized that *H. biforata* and *H. biseriata* are synonyms. We recover them as sister species with differing relatively long branch lengths and a bs of 96%. However, our analysis does not give a clear resolution to this issue and further studies are necessary to resolve the status of these two species.

Not many hypotheses have been put forth regarding the relationship of species within *Aristocypha*. However, we found *A. spuria* and *A. fenestrella* to be closely related. Wilson et al. (2008) and Hämäläinen et al. (2009) proposed this same relationship based on morphological similarities between the two species notably, the shape and the color of the mesothoracic triangle and the presence of yellow stripes on the ventral side of the synthorax. However, *A. baibarana*, not included here, has also been proposed to be sister to *A. fenestrella* (Hämäläinen and Yeh 1998; Wilson and Reels 2001). The two species are differentiated by the presence of azure blue patches on the male abdomen of *A. baibarana* as opposed to the completely dark abdomen of *A. fenestrella*. In the female, the markings on the poststernum and the abdominal segments 2–7 are also different (Hämäläinen and Yeh 1998).

In the current project, three out of the five monotypic genera were not included: *Calocypha*, *Heterocypha*, *Sclerocypha*. Van Tol and Günther (2018) hypothesized that *Sclerocypha* was a member of *Libellago* because of some morphological similarities, notably: the absence of an opaque band around the nodus, the absence of secondary antenodal crossveins, the presence of five antenodal crossveins instead of nine and the anal vein originating proximal to the first antenodal (van Tol 2007). Günther (2019) supported that hypothesis with behavioral similarities between the two genera. For example, Günther (2019) suggested that the stationary presentation of forewings in *Sclerocypha* is homologous to the stationary wing display reported in *Libellago* species by Orr (1996). Other similarities include male aggregations sensu Günther (2008) and the complete submersion of females during oviposition (Günther 2019). We have followed this hypothesis by synonymizing this genus into *Libellago.* For both *Calocypha* and *Heterocypha*, it remains unknown where they potentially fit among Chlorocyphidae. They are currently classified as members of Rhinocyphinae due to their similarities with other genera from the subfamily (Dijkstra et al. 2014). The preliminary results obtained from the COI gene only show that the genus *Calocypha* is embedded within the genus *Rhinocypha*. Regarding *Heterocypha*, we are unsure how it would fit within Rhinocyphinae or potentially within the family. It will be necessary to include taxa representing these two genera in future analyses to fully test the hypothesis of their classification.

In conclusion, we propose an updated classification scheme for the family of Chlorocyphidae. We describe two new genera, two new subfamilies, and address the classification of species among both. However, in Libellaginae and Rhinocyphinae, further studies (including morphological and molecular work) are required to stabilize the classification in those subfamilies. Our phylogeny provides a robust framework for future evolutionary research focused on the morphology, coloration, and behavior of this unique family of damselflies.

5. Systematics

The most recent classification of Chlorocyphidae is available in Dijkstra et al. (2014, 2013). In the revised classification below, we propose reclassifying 26 species due to the non-monophyly of genera, of which 17 are placed in two new genera: *Scapanocypha* **gen. nov.** and *Ebenocypha* **gen. nov.** (Tables 2, 3). We also recommend using *Paracypha unimaculata* instead of *Rhinocypha unimaculata*. Furthermore, we propose to define the six main clades found in our phylogeny as subfamilies. For four of these clades existing names are available (Chlorocyphinae, Disparocyphinae, Libellagininae, Rhinocyphinae). For the other two, we establish new subfamilies (Cyranoinae **subfam. nov.**, Indocyphinae **subfam. nov.**). The names Disparocyphinae and Libellagininae are older than the family name, which is the reason why Dijkstra et al. (2014) refrained from using the subfamily names. For the sake of nomenclatural stability, we ignore this nomenclatural conundrum and keep using Chlorocyphidae as the family name. The following list provides the distribution of genera amongst the subfamilies:

Chlorocyphinae Cowley, 1937: *Africocypha* Pinhey, 1961, *Chlorocypha* Fraser, 1928, *Platycypha* Fraser, 1949, *Stenocypha* Dijkstra, 2013.

Cyranoinae Fomekong-Lontchi, Kalkman and Bybee **subfam. nov.**: *Cyrano* Needham and Gyger, 1939.

Disparocyphinae Munz, 1919: *Disparocypha* Ris, 1916.

Indocyphinae Fomekong-Lontchi, Kalkman and Bybee **subfam. nov.**: *Indocypha* Fraser, 1949.

Libelligininae Jacobson and Bianchi, 1905: *Libellago* Selys, 1840.

Rhinocyphinae Bechly, 1996: *Aristocypha* Laidlaw, 1950, *Calocypha* Fraser, 1928, *Ebenocypha* Fomekong-Lontchi, Kalkman and Bybee **gen. nov.**, *Heliocypha* Fraser, 1949, *Heterocypha* Laidlaw, 1950, *Paracypha* Fraser, 1949, *Rhinocypha* Rambur, 1842, *Scapanocypha* Fomekong-Lontchi, Kalkman and Bybee **gen. nov.**, *Sundacypha* Laidlaw, 1950.

Table 2. List of synonymized genera.

Synonymised genus	Synonymised with
Melanocypha	*Libellago*
Pachycypha	*Libellago*
Rhinoneura	*Rhinocypha*
Sclerocypha	*Libellago*
Watuwila	*Libellago*

Table 3. List of reclassified species.

New generic placement	Former combination	Proposed new combination
Chlorocypha	*Africocypha varicolor*	*Chlorocypha varicolor*
Heliocypha	*Aristocypha iridea*	*Heliocypha iridea*
	Rhinocypha xanthe	*Heliocypha xanthe*
Libellago	*Melanocypha snellemanni*	*Libellago snellemanni*
	Pachycypha aurea	*Libellago aurea*
	Sclerocypha bisignata	*Libellago bisignata*
	Watuwila vervoorti	*Libellago vervoorti*
Ebenocypha **gen. nov.**	*Rhinocypha anisoptera*	*Ebenocypha anisoptera*
	Rhinocypha ignipennis	*Ebenocypha ignipennis*
	Rhinocypha heterostigma	*Ebenocypha heterostigma*
	Rhinocypha orea	*Ebenocypha orea*
	Rhinocypha pallidifrons	*Ebenocypha pallidifrons*
	Rhinocypha peitho	*Ebenocypha peitho*
	Rhinocypha pelops	*Ebenocypha pelops*
	Rhinocypha seducta	*Ebenocypha seducta*
	Rhinocypha selysi	*Ebenocypha selysi*
	Rhinocypha trimaculata	*Ebenocypha trimaculata*
	Rhinocypha watsoni	*Ebenocypha watsoni*
Rhinocypha	*Rhinoneura caerulea*	*Rhinocypha caerulea*
	Rhinoneura villosipes	*Rhinocypha villosipes*
Scapanocypha **gen. nov.**	*Rhinocypha arguta*	*Scapanocypha arguta*
	Rhinocypha drusilla	*Scapanocypha drusilla*
	Rhinocypha huai	*Scapanocypha huai*
	Rhinocypha ogasawarensis	*Scapanocypha ogasawarensis*
	Rhinocypha uenoi	*Scapanocypha uenoi*
	Rhinocypha taiwana	*Scapanocypha taiwana*

We include a description of the key characters of all genera and a list of species, including the newly described genera. Species included in our taxon sampling are indicated with an asterisk.

Africocypha Pinhey, 1961

Morphological traits. (Pinhey 1961) The anal appendages of *Africocypha* differ from other African Chlorocyphidae by cerci being slightly longer than the paraprocts. The cerci present an exfoliation of the outside and the tips have one indentation on the underside. The base of the paraprocts is very broad and narrows sharply toward the tip.

Type species. *Africocypha greyi* Pinhey, 1961.

Revised classification. *Africocypha varicolor* is moved to *Chlorocypha*.

Number of species and notes on distribution and ecology. Two species, distribution limited to Lower Guinea (Cameroon, Equatorial Guinea, Gabon, Nigeria) (Dijkstra 2017). They inhabit rocky rivers at higher elevations (de Vries et al. 2024).

Included species. *Africocypha centripunctata* (Gambles, 1975) — *Africocypha lacuselephantum* (Karsch, 1899)*.

Aristocypha Laidlaw, 1950

Morphological traits. Species in *Aristocypha* are characterized by broad wings in the male with a ratio of length to width between 4:1 and 3:1; the network of wing venation is dense; the cells are more elongated transversely toward the tip of the wing; and the pink, purple or yellowish mesothoracic triangle is enlarged and completely covers the middorsal carina on its entire length (Laidlaw 1950) but bordering triangular “epaulets” as found in *He-*

liocypha are absent. Hämäläinen et al. (2009) noted that the mesothoracic triangle is the most important defining feature of the genus.

Type species. *Rhinocypha quadrimaculata* Selys, 1853; included in the topology.

Revised classification. Our phylogeny recovered *Aristocypha iridea* (Selys, 1891) as a member of *Heliocypha*, and it is then reclassified as *Heliocypha iridea*.

Number of species and notes on distribution and ecology. 11 species, found in the tropical part of mainland Asia (Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Pakistan, Taiwan, Thailand, and Vietnam). Little information is available for the ecology of the genus. Some species are known to inhabit shallow and semi-shaded forest streams and montane streams (Hämäläinen and Yeh 1998; Zhang 2019). They are reported to be shy as they fly away as soon as they are disturbed (Hämäläinen and Yeh 1998).

Included species. *Aristocypha aino* Hämäläinen, Reels and Zhang, 2009* — *Aristocypha baibarana* (Matsumura, 1931) — *Aristocypha chaoi* (Wilson, 2004)* — *Aristocypha cuneata* (Selys, 1853) — *Aristocypha fenestrella* (Rambur, 1842)* — *Aristocypha fulgipennis* (Guérin, 1831)* — *Aristocypha hilaryae* (Fraser, 1927) — *Aristocypha immaculata* (Selys, 1879)* — *Aristocypha quadrimaculata* (Selys, 1853)* — *Aristocypha spuria* (Selys, 1879)* — *Aristocypha trifasciata* (Selys, 1853).

Calocypha Fraser, 1928

Morphological traits. The wings of *Calocypha* are petiolated, the petiole ending distally to the proximal end of the discoidal cell; the fore- and hindwings are equal in shape with rounded tips; the distal ⅓ of the wings are black with a straight margin; the nervation in that portion of the wing is less dense; the cerci are two times longer than S10, curved at the tips and bluntly pointed and holding a light pilosity; the paraprocts are two times shorter than the cerci and hold tiny spines on their upper side (Fraser 1924a, 1928b).

Type species. *Calocypha laidlawi* (Fraser, 1924); not included in the topology.

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. One species, only known from the Western Ghats (India) (Kalkman et al. 2020), found in shaded portions of streams/rivers on vegetation of submerged logs (Fraser 1924a).

Included species. *Calocypha laidlawi* (Fraser, 1924a).

Chlorocypha Fraser, 1928

Morphological traits. The legs are largely black; abdomen broad with S3 less than two times longer than wide; medium size (Hw 18–27 mm) (Dijkstra and Clausnitzer 2014).

Type species. *Agrion dispar* Palisot de Beauvois, 1807; included in the topology.

Revised classification. *Africocypha varicolor* is reclassified as *Chlorocypha*.

Number of species and notes on distribution and ecology. 30 species, restricted to tropical Africa (West and Central Africa mainly); they live in forested running waters, except for *C. curta*, which also can be found in disturbed and dry open habitats (Dijkstra and Clausnitzer 2014).

Included species. *Chlorocypha aphrodite* (Le Roi, 1915)* — *Chlorocypha aurora* Dijkstra, Kipping and Schütte in Dijkstra, Kipping and Mézière, 2015 — *Chlorocypha cancellata* (Selys, 1879)* — *Chlorocypha consueta* (Karsch, 1899b)* — *Chlorocypha curta* (Hagen in Selys, 1853) — *Chlorocypha cyanifrons* (Selys, 1873)* — *Chlorocypha dahli* Fraser, 1956 — *Chlorocypha dispar* (Palisot de Beauvois, 1807)* — *Chlorocypha fabamacula* Pinhey, 1961 — *Chlorocypha flammea* Dijkstra and Clausnitzer in Dijkstra, Kipping and Mézière, 2015 — *Chlorocypha frigida* Pinhey, 1961* — *Chlorocypha ghesquierei* Fraser, 1959 — *Chlorocypha glauca* (Selys, 1879) — *Chlorocypha granata* Dijkstra in Dijkstra, Kipping and Mézière, 2015 — *Chlorocypha helenae* Legrand, 1984* — *Chlorocypha jejuna* (Karsch, 1898) — *Chlorocypha luminosa* (Karsch, 1893) — *Chlorocypha maxima* Dijkstra, Kipping and Mézière in Dijkstra, Kipping and Mézière, 2015 — *Chlorocypha neptunus* (Sjöstedt, 1900) — *Chlorocypha pyriformosa* Fraser, 1947 — *Chlorocypha radix* Longfield, 1959 — *Chlorocypha rubida* (Hagen in Selys, 1853)* — *Chlorocypha schmidti* Pinhey, 1967 — *Chlorocypha selysi* (Karsch, 1899a) — *Chlorocypha seydeli* Fraser, 1958 — *Chlorocypha trifaria* (Karsch, 1899a) — *Chlorocypha varicolor* (Dijkstra, Kipping and Günther in Dijkstra, Kipping and Mézière, 2015)* [*Africocypha varicolor* Dijkstra, Kipping and Günther in Dijkstra, Kipping and Mézière, 2015] — *Chlorocypha victoriae* (Förster, 1914)* — *Chlorocypha wittei* Fraser, 1955.

Cyrano Needham and Gyger, 1939

Morphological traits. Stout body, the base of the abdomen is swollen, postclypeus is wider than long, number of ante- and postnodal crossveins almost the same, nodus is halfway to the pterostigma, arculus distal to the third antenodal (Hämäläinen 1989; Needham and Gyger 1939).

Type species. *Rhinocypha unicolor* Hagen in Selys, 1869; included in the topology.

Revised classification. No change in this genus.

Number of species and notes on distribution and ecology. Two species, endemic to the Philippines (Hämäläinen 1989).

Included species. *Cyrano angustior* Hämäläinen, 1989* — *Cyrano unicolor* (Hagen in Selys, 1869)*.

Disparocypha Ris, 1916

Morphological traits. The single known species of *Disparocypha* is characterized by a less pronounced anteclypeus and postclypeus. The wings are narrow with an elongated petiole, a reduced Cu_1 and an absent Cu_2. Also, the proximal side of the pterostigma is narrower than the distal side (Fraser 1949; Ris 1916).

Type species. *Disparocypha biedermanni* Ris, 1916; included in the topology

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. One species, endemic to Sulawesi (Günther 2020). *Disparocypha biedermanni* oviposits in large logs and mossy barks away from the stream (Günther 2008) and is reported for not displaying any courtship behavior (Günther 2008).

Included species. *Disparocypha biedermanni* Ris, 1916*.

Ebenocypha Fomekong-Lontchi, Kalkman and Bybee gen. nov.

https://zoobank.org/C1DBAA04-2D08-43D4-9D93-33F82713A25F

Type species. *Rhinocypha anisoptera* Selys, 1879; included in the topology

Etymology. From Greek ἔβενος (*ébenos*) "ebony" referring to the dark, ebony-like body of species in this genus; and *-cypha* which is the suffix generally added to genera names in Chlorocyphidae.

Diagnosis. Characterized by an all black abdomen. The hindwing is broader than the forewing, and is either completely or partly opaque and iridescent (Hämäläinen 2017). At least part of the hindwing presents a melanization pattern while the forewing is completely transparent. The thorax is black with yellow to orange stripes. A pink, purple or yellowish colored mesothoracic triangle such as found in *Aristocypha*, *Heliocypha* and *Rhinocypha* is absent.

Comments. Six out of the eleven species known in this new genus were included in our tree, and all form a monophyletic clade. They are included in the subfamily Rhinocyphinae. Information on the biology and the ecology of the species is limited. However, *Ebenocypha watsoni* **comb. nov.** is known from grassy and rocky streams, around logged forests (van Tol and Rozendaal 1995). *Ebenocypha seducta* **comb. nov.** is known from slow moving mountain streams around 1200 m a.s.l in Vietnam (Hämäläinen and Karube 2001a).

Distribution. The genus is known from Java, Sumatra, Peninsular Malaysia, Thailand, Vietnam reaching northwest as far as Bangladesh and Assam. The genus has not been recorded from China, Cambodia and in India is not known to occur west of the Bramaputra.

Included species. *Ebenocypha anisoptera* (Selys, 1879)* **comb. nov.** [*Rhinocypha anisoptera* Selys, 1879] — *Ebenocypha ignipennis* (Selys, 1879) **comb. nov.** [*Rhinocypha ignipennis* Selys, 1879] — *Ebenocypha heterostigma* (Rambur, 1842) **comb. nov.** [*Rhinocypha heterostigma* Rambur, 1842] — *Ebenocypha orea* (Hämäläinen and Karube, 2001)* **comb. nov.** [*Rhinocypha orea* Hämäläinen and Karube, 2001] — *Ebenocypha pallidifrons* (Ris, 1927)* **comb. nov.** [*Rhinocypha pallidifrons* Ris, 1927] — *Ebenocypha peitho* (Hämäläinen, 2017) **comb. nov.** [*Rhinocypha peitho* Hämäläinen, 2017] — *Ebenocypha pelops* (Laidlaw, 1936)* **comb. nov.** [*Rhinocypha pelops* Laidlaw, 1936] — *Ebenocypha seducta* (Hämäläinen and Karube, 2001)* **comb. nov.** [*Rhinocypha seducta* Hämäläinen and Karube, 2001] — *Ebenocypha selysi* (Krüger, 1898) **comb. nov.** [*Rhinocypha selysi* Krüger, 1898] — *Ebenocypha trimaculata* (Selys, 1853) **comb. nov.** [*Rhinocypha trimaculata* Selys, 1853] — *Ebenocypha watsoni* (van Tol and Rozendaal, 1995)* **comb. nov.** [*Rhinocypha watsoni* van Tol and Rozendaal, 1995].

Heliocypha Fraser, 1949

Morphological traits. This genus is characterized by the presence of a pink, purple or yellowish mesothoracic triangle which extends up to the middle of the dorsum, and bordered by triangular "epaulets" of the same color (Fraser 1949). The colored dorsal mesothoracic triangle is shorter than in *Aristocypha*. In *Heliocypha*, the melanization of the hindwing stops before the tip while they extend all the way to the tip in *Aristocypha* (Zhang 2019).

Type species. *Rhinocypha bisignata* Hagen in Selys, 1853; included in the topology.

Revised classification. *Rhinocypha xanthe* is renamed as *Heliocypha xanthe*. *Aristocypha iridea* is reclassified as *Heliocypha iridea*.

Number of species and notes on distribution and ecology. The genus includes 11 species found in the Indian subcontinent, mainland southeast Asia (including

Taiwan and Hainan) and Sundaland (Sumatra, Borneo, Java and Bali). They inhabit streams in forest (disturbed and undisturbed). Some species are found in fast flowing water with sandy, rocky, gravelly or a variety of substrates (R. Dow pers. comm.).

Included species. *Heliocypha angusta* (Hagen in Selys, 1853)* — *Heliocypha biforata* (Selys, 1859)* — *Heliocypha biseriata* (Selys, 1859)* — *Heliocypha bisignata* (Hagen in Selys, 1853)* — *Heliocypha fenestrata* (Burmeister, 1839) — *Heliocypha iridea* (Selys, 1891)* **comb. nov.** [*Aristocypha iridea* (Selys, 1891)] [*Rhinocypha iridea* Selys, 1891] — *Heliocypha mariae* (Lieftinck, 1930) — *Heliocypha nubecula* (Lieftinck, 1948) — *Heliocypha perforata* (Percheron in Guérin and Percheron, 1835)* — *Heliocypha vantoli* Hämäläinen, 2016* — *Heliocypha xanthe* **comb. nov.** (Ris, 1927)* [*Rhinocypha xanthe* Ris, 1927].

Heterocypha Laidlaw, 1950

Morphological traits. *Heterocypha vitrinella* has broad wings, with length approximately four times longer than the breadth; the mesothoracic triangle is broad and stops halfway through the mid-dorsal carina (Fraser 1935; Laidlaw 1950).

Type species. *Rhinocypha vitrinella* Fraser, 1935; not included in the topology.

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. One species, known from Northeast India (Fraser 1935; Joshi et al. 2022; Kalkman et al. 2020) and also reported in eastern China (Yunnan) (Zhang 2019). It inhabits dirty and stagnant water bodies in rainforests (Lahiri 1987).

Included species. *Heterocypha vitrinella* (Fraser, 1935).

Indocypha Fraser, 1949

Morphological traits. Generally medium to large size, with a dorsoventrally flattened abdomen. The wings are hyaline; the anal vein (1A) reaches the wing margin proximal to the first antenodal (Zhang et al. 2010).

Type species. *Libellago asiatica vittata* Selys, 1891; included in the topology.

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. The seven species are generally rare and elusive. They are found in fast flowing rivers and streams at lower elevations in forested areas. They are present in southern China and surrounding areas in Vietnam, Laos, Thailand, and Myanmar (Hämäläinen 2014; Zhang et al. 2018, 2010).

Included species. *Indocypha catopta* Zhang, Hämäläinen and Tong, 2010* — *Indocypha cyanicauda* Zhang and Hämäläinen in Zhang et al., 2018* — *Indocypha katharina* (Needham, 1930)* — *Indocypha neglecta* Hämäläinen, 2014 — *Indocypha silbergliedi* Asahina, 1988 — *Indocypha svenhedini* (Sjöstedt, 1932) — *Indocypha vittata* (Selys, 1891)*.

Libellago Selys, 1840

Morphological traits. A good morphological description of *Libellago* was provided by Fraser (1949) and updated by van Tol (2007). The tips of the forewings of the male usually bear dark markings and lack a pterostigma; while the hindwings are transparent have a pterostigma. The wings have at most 6 antenodals. The sectors of the arculus start at the same point; and the arculus itself is bent at a right angle halfway through.

Type species. *Calopteryx lineata* Burmeister, 1839; not included in the topology.

Revised classification. *Watuwila vervoorti*, *Sclerocypha bisignata*, *Pachycypha aurea* are reclassified as *Libellago*.

Number of species and notes on distribution and ecology. 27 species, distributed from India and Sri-Lanka in the west to southern China and Taiwan (mostly the north) in the east, including Myanmar, Thailand, Malaysia, Singapore, Brunei and Indonesia. They are forest species in highland or lowland forests, lotic environments. They have been reported in a diverse set of habitats including mountain streams, swamp waters, forest streams, fast flowing rivers (Dow and Hämäläinen 2008; Fraser 1939; Orr 2009, 2004). The females oviposit in submerged logs when the water levels are low enough to expose them (Orr 2009; van Tol 2007), but also in midribs of leaves floating in streams as well as small pieces of dead wood (R. Dow pers. comm.).

Included species. *Libellago adami* Fraser, 1939* — *Libellago andamanensis* (Fraser, 1924) — *Libellago aurea* (Lieftinck, 1950)* **comb. nov.** [*Pachycypha aurea* Lieftinck, 1950] — *Libellago asclepiades* (Ris, 1916)* — *Libellago aurantiaca* (Selys, 1859)* — *Libellago balus* Hämäläinen, 2002* — *Libellago bisignata* (McLachlan, 1870) **comb. nov.** [*Sclerocypha bisignata* (McLachlan, 1870)] [*Micromerus bisignatus* McLachlan, 1870] — *Libellago blanda* (Hagen in Selys, 1853)* — *Libellago celebensis* van Tol, 2007* — *Libellago corbeti* van der Poorten, 2009 — *Libellago daviesi* van Tol, 2007* — *Libellago dorsocyana* Lieftinck, 1937* — *Libellago finalis* (Hagen in Selys, 1869) — *Libellago greeni* (Laidlaw, 1924)* — *Libellago hyalina* (Selys, 1859)* — *Libellago indica* (Fraser, 1928a) — *Libellago lineata* (Burmeister, 1839) — *Libellago manganitu* van Tol, 2007* — *Libellago naias* Lieftinck, 1932 — *Libellago orri* Dow and Hämäläinen, 2008 — *Libellago phaethon* (Laidlaw, 1931)

— *Libellago rufescens* (Selys, 1873)* — *Libellago semiopaca* (Selys, 1873)* — *Libellago snellemanni* (Albarda in Selys, 1879)* **comb. nov.** [*Melanocypha snellemanni* (Albarda in Selys, 1879)] [*Micromerus snellemanni* Albarda in Selys, 1879] — *Libellago stictica* (Selys, 1869)* — *Libellago stigmatizans* (Selys, 1859)* — *Libellago sumatrana* (Albarda in Selys, 1879)* — *Libellago vervoorti* (van Tol, 1998)* **comb. nov.** [*Watuwila vervoorti* van Tol, 1998] — *Libellago xanthocyana* (Selys, 1869).

Paracypha Fraser, 1949

Morphological traits. Characterized by the presence of two rows of cells that separate the margin of the hind wing and the anal vein (Fraser 1949; Laidlaw 1950). The hindwing has a metallic green patch that extends from slightly after the nodus to halfway between the nodus and the pterostigma. The forewings are hyaline at the base, and switch to a brown metallic after the nodus. The hindwings are hyaline at the base, and metallic brown after the nodus, but with a large vitreous band (Selys 1854, 1853).

Type species. *Rhinocypha unimaculata* Selys, 1853; included in the topology.

Revised classification. No change in this genus.

Number of species and notes on distribution and ecology. One species, known from Bhutan, India, Pakistan, and Nepal (Kalkman et al. 2020). It lives in the running waters of the Himalayas (Conniff 2020) and stays in small spaces under small stones and pebbles (Kumar 1973).

Included species. *Paracypha unimaculata* (Selys, 1853)*.

Platycypha Fraser, 1949

Morphological traits. Differing from other African chlorocyphids by wider male tibiae and a largely colored abdomen (Dijkstra and Clausnitzer 2014). However, the group of "blue *Platycypha*", endemic to Angola have less wide tibiae and lack the yellowish or reddish marking found in other *Platycypha* tibiae (Kipping et al. 2017).

Type species. *Libellago caligata* Selys, 1853; included in the topology.

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. 9 species, limited to the tropical part of Africa (Dijkstra and Clausnitzer 2014). They are found on running shaded forest streams, submontane habitats, lakes, sandy and rocky streams and lakes (Dijkstra and Clausnitzer 2014; Pinhey 1982).

Included species. *Platycypha amboniensis* (Martin, 1915) — *Platycypha angolensis* Longfield, 1959* — *Platycypha auripes* (Förster, 1906)* — *Platycypha bamptoni* (Pinhey, 1975) — *Platycypha caligata* (Selys, 1853)* — *Platycypha crocea* (Longfield, 1947)* — *Platycypha eliseva* Dijkstra, 2008* — *Platycypha fitzsimonsi* (Pinhey, 1950)* — *Platycypha inyangae* Pinhey, 1958* — *Platycypha lacustris* (Förster, 1914) — *Platycypha picta* (Pinhey, 1962)* — *Platycypha pinheyi* Fraser, 1950 — *Platycypha rubriventris* (Pinhey, 1975) — *Platycypha rufitibia* (Pinhey, 1961a)*.

Rhinocypha Rambur, 1842

Morphological traits. The following characters characterize *Rhinocypha*: mesothoracic triangle short, abdomen with black markings associated with other paler colors: red, yellow, blue or purple, quadrilateral divided in at least 3 subcells, smoky or black patches of variable proportion on the wings with sometimes reflective wing patterns.

Type species. *Rhinocypha tincta* Rambur, 1842; included in the topology.

Revised classification. The definition of the genus *Rhinocypha* has changed a lot over the years. Initially described by Rambur (1842), the description was updated by Fraser (1949). The genus was later split by Laidlaw (1950) to accommodate the genera *Aristocypha*, *Calocypha*, *Heliocypha*, *Heterocypha* and *Sundacypha*. Herein, we split the genus *Rhinocypha* again in three with the description of two new genera (*Ebenocypha* **gen. nov.** and *Scapanocypha* **gen. nov.**). We also propose to use *Paracypha unimaculata* in place of *Rhinocypha unimaculata*.

Number of species and notes on distribution and ecology. We assign 29 species to *Rhinocypha*. The genus is found in the Philippines, Borneo, Sulawesi, Moluccas, New Guinea eastwards to the Solomon Islands. *Rhinocypha* is the only genus in the family for which the range extends to the Solomon Islands (Kalkman and Orr 2013). Species can live in open and shaded streams, either in primary or secondary forests. Depending on the species, they occur in fast flowing waters or in quiet spots in rivers, and some can tolerate some level of disturbance (van Tol and Günther 2018).

Included species. *Rhinocypha aurofulgens* Laidlaw, 1931* — *Rhinocypha aurulenta* Förster, 1903 — *Rhinocypha colorata* Hagen in Selys, 1869 — *Rhinocypha caerulea* (Kimmins, 1936) **comb. nov.** [*Rhinoneura caerulea* Kimmins, 1936] — *Rhinocypha cucullata* Selys, 1873* — *Rhinocypha dorsosanguinea* Lieftinck, 1961 — *Rhinocypha flavipoda* van Tol and Günther, 2018 — *Rhinocypha frontalis* Selys, 1873 — *Rhinocypha hageni* Krüger, 1898 — *Rhinocypha humeralis* Selys, 1873* — *Rhinocypha latimacula* Lieftinck, 1974

— *Rhinocypha liberata* Lieftinck, 1949* — *Rhinocypha monochroa* Selys, 1873 — *Rhinocypha moultoni* Laidlaw, 1915 — *Rhinocypha pagenstecheri* Förster, 1897 — *Rhinocypha pelengensis* van Tol and Günther, 2018 — *Rhinocypha phantasma* Lieftinck, 1935 — *Rhinocypha sangihensis* van Tol and Günther, 2018* — *Rhinocypha sanguinolenta* Lieftinck, 1961* — *Rhinocypha spinifer* Laidlaw, 1931* — *Rhinocypha stygia* Förster, 1897* — *Rhinocypha sumbana* Förster, 1897 — *Rhinocypha tincta* Rambur, 1842* — *Rhinocypha togeanensis* van Tol and Günther, 2018 — *Rhinocypha turconii* Selys, 1891* — *Rhinocypha ustulata* Brauer, 1867 — *Rhinocypha villosipes* (Laidlaw, 1915)* **comb. nov.** [*Rhinoneura villosipes* Laidlaw, 1915] — *Rhinocypha viola* Orr, 2002* — *Rhinocypha virgulata* van Tol and Günther, 2018.

Scapanocypha Fomekong-Lontchi, Kalkman and Bybee gen. nov.

https://zoobank.org/C2388ED1-B659-4E5B-AD96-6EF7C0251291

Type species. *Rhinocypha drusilla* Needham, 1930; included in the topology.

Etymology. The first part of the name comes from Greek σκαπάνη (skapánē) meaning "spade", which refers to the characteristic red spade marking on S2. The second part is the suffix *-cypha*, which is generally used to name genera of the family Chlorocyphidae.

Diagnosis. This new genus includes the species of the *Rhinocypha drusilla* group. These are distinguishable by the combination of a reddish to orange dorsum of the abdomen, and a red spade-shaped marking on the black dorsum of S2. S1 is also mostly black. The thorax lacks a large pink, purple or yellowish colored mesothoracic triangle such as found in *Aristocypha*, *Heliocypha* and *Rhinocypha*. Wang et al. (2013) presented an extensive description of the group.

Comments. Our phylogeny recovered this group as monophyletic, with 4 of its 6 species having been included.

Distribution and ecology. The distribution is limited to North Thailand, Yunnan and Northern Vietnam (*R. arguta*), Hainan (*R. huai*), Southern and Central mainland China (*R. drusilla*), Ogasawara islands (*R. ogasawarensis*), North Taiwan (*R. taiwana*) and Iriomote island (*R. uenoi*) (Wang et al. 2013; Zhang 2019; M. Hämäläinen, pers. comm.). They live in rocky streams, and will only show up when the sun is shining (Hämäläinen and Divasiri 1997; Wang et al. 2013).

Included species. *Scapanocypha arguta* (Hämäläinen and Divasiri, 1997)* **comb. nov.** [*Rhinocypha arguta* Hämäläinen and Divasiri, 1997] — *Scapanocypha drusilla* (Needham, 1930)* **comb. nov.** [*Rhinocypha drusilla* Needham, 1930] — *Scapanocypha huai* (Zhou and Zhou, 2006) **comb. nov.** [*Heliocypha huai* Zhou and Zhou, 2006] [*Rhinocypha huai* (Zhou and Zhou, 2006)] — *Scapanocypha ogasawarensis* (Oguma, 1913)* **comb. nov.** [*Rhinocypha ogasawarensis* Oguma, 1913] — *Scapanocypha taiwana* (Wang and Chang in Wang et al., 2013)* **comb. nov.** [*Rhinocypha taiwana* Wang and Chang in Wang, Cherng, Chang and Jiang, 2013] — *Scapanocypha uenoi* (Asahina, 1964) **comb. nov.** [*Rhinocypha uenoi* Asahina, 1964].

Stenocypha Dijkstra, 2013

Morphological traits. This genus represents the *gracilis*-group of *Chlorocypha* as defined by Pinhey (1967). Species differ from *Chlorocypha* by a slender abdomen, S3 is about three times longer than wide (Dijkstra 2013).

Type species. *Libellago gracilis* Karsch, 1899; included in the topology.

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. 5 species are recognized. They inhabit forested streams of Albertine rift, with the exception of *S. gracilis*, which is found in Central Africa (Dijkstra 2013; Dijkstra and Clausnitzer 2014).

Included species. *Stenocypha gracilis* (Karsch, 1899)* — *Stenocypha hasta* (Pinhey, 1960) — *Stenocypha jacksoni* (Pinhey, 1952)* — *Stenocypha molindica* (Fraser, 1948) — *Stenocypha tenuis* (Longfield, 1936)*.

Sundacypha Laidlaw, 1950

Morphological traits. The apex of the hindwing is more rounded than the forewings, the vein 1A reaches the wing border distally to the arculus and the mid-dorsal carina is four times longer than the mesothoracic triangle (Laidlaw 1950; Orr 1999).

Type species. *Rhinocypha petiolata* Selys, 1859; included in the topology.

Revised classification. No changes in this genus.

Number of species and notes on distribution and ecology. 2 species recognized. *Sundacypha petiolata* is found throughout most of Sundaland, while *Sundacypha striata* is restricted to Borneo. They inhabit streams with steep banks in swampy forests (*S. striata*) and small forest streams or backwater with silty substrates (*S. petiolata*) (Orr 1999).

Included species. *Sundacypha petiolata* (Selys, 1859)* — *Sundacypha striata* Orr, 1999*.

6. Declarations

Authors' contributions. Conceptualization, JF-L, VJK and SMB; methodology, JF-L, PF and SMB; preparing, writing, review and editing, JF-L, VJK, PF, JLW, JCA, RG, K-DBD., MH, RD and SMB; supervision, SMB; resources and funding acquisition, JF-L, VJK, PF, JLW, JCA, RG and SMB.

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Data availability. The data underlying this article is uploaded to the Dryad Digital Repository (https://doi.org/10.5061/dryad.s4mw6m9kj).

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Supplementary Material 1

Files S1–S3

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Data type: .zip

Explanation notes: File S1. Quartet topology counts for internal nodes in the Quartet Sampling analysis [.txt file]. — **File S2.** Quartet Sampling support metrics for internal nodes and terminal taxa [.csv file]. — **File S3.** Phylogenetic tree annotated with Quartet Sampling node identifiers and Quartet Fidelity scores [.tre file].

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