

Article

The First Report of a Non-Canonical Telomeric Motif in Neuroptera: (TTGGG)*n* in Chromosomes of *Nineta flava* (Scopoli, 1763), Chrysopidae

Desislava Stoianova ^{1,2,*}  and Snejana Grozeva ¹ 
¹ Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 1000 Sofia, Bulgaria; sngrov@gmail.com

² National Museum of Natural History, Bulgarian Academy of Sciences, 1000 Sofia, Bulgaria

* Correspondence: d.st.stoianova@gmail.com

Abstract

Background: Telomeres are nucleoprotein complexes that maintain chromosome integrity in eukaryotes. In insects, the canonical telomeric repeat (TTAGG)*n* is considered ancestral, though alternative motifs exist across various orders. Neuroptera, comprising about 5800 species, remains understudied regarding telomeric sequences, with data available for only seven species across three families. Previous studies reported the absence of (TTAGG)*n* in Chrysopidae species, contrasting with its presence in other Neuroptera families. This study aimed to identify and characterize telomeric motifs in Chrysopidae using chromosome-level genome assemblies and search for retrotransposon insertions. **Methods:** We analyzed chromosome-level genome assemblies from four Chrysopidae species: three Chrysopinae—*Chrysoperla carnea* (Stephens, 1836), *Chrysopa pallens* (Rambur, 1838), and *Nineta flava* (Scopoli, 1763); and one Nothochrysininae—*Nothochrysa capitata* (Fabricius, 1793). Terminal sequences of chromosome pseudomolecules were examined using Geneious Prime[®], applying five specific criteria for optimal telomeric sequence identification. We searched for SART and TRAS retrotransposons using the graphical sequence panel in GenBank. **Results:** We identified (TTGGG)*n* as the telomeric motif in *N. flava*, representing the first report of this pentanucleotide repeat in telomeres of Neuroptera. Arrays ranged from 228 to 8005 bp across seven terminal locations in five chromosome pseudomolecules. In *N. capitata*, we detected (TTAGG)*n* arrays (2316–3808 bp) at four terminal locations. No telomeric motifs meeting all criteria were found in *C. carnea* and *C. pallens*. No SART/TRAS retrotransposons were detected in any species. **Conclusions:** This study reveals previously unknown telomeric diversity within Chrysopidae, with both canonical (TTAGG)*n* and novel (TTGGG)*n* motifs present. The discovery of (TTGGG)*n* in Neuroptera expands known telomeric sequence diversity in this order.

Keywords: chromosome structure; Chrysopinae; genome assembly; Nothochrysininae; (TTAGG)*n*; insect cytogenetics



Academic Editor: Pedro Lorite Martínez

Received: 24 August 2025

Revised: 17 September 2025

Accepted: 22 September 2025

Published: 14 October 2025

Citation: Stoianova, D.; Grozeva, S. The First Report of a Non-Canonical Telomeric Motif in Neuroptera: (TTGGG)*n* in Chromosomes of *Nineta flava* (Scopoli, 1763), Chrysopidae. *Genes* **2025**, *16*, 1201. <https://doi.org/10.3390/genes16101201>

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

Telomeres are nucleoprotein complexes at chromosome ends of eukaryotes that maintain chromosome end integrity and contribute to genome stability [1–4]. In most eukaryotes, telomeric DNA consists of short G-rich tandem repeats—typically 5–8 bp [5]—bound by telomere-binding proteins that assemble a protective end cap [2,4]. In vertebrates, the hexameric repeat (TTAGGG)*n* predominates [6]. In insects, the telomeric repeat (TTAGG)*n*

forms tandem arrays at chromosome ends [7–9]. This motif is considered ancestral for Insecta because it was found in most major insect orders and is conserved in basal apterous insect orders, and its phylogenetic distribution pattern supports it being an ancestral motif that was lost repeatedly during insect evolution [7]. The motif is widespread but not universal, since independent losses or replacements occur in multiple lineages (e.g., Diptera, Lepidoptera, many Heteroptera; diverse motifs in Hymenoptera) [10,11]. Many insects carry alternative repeats 1–11 bp long. Some Diptera families, such as Syrphidae and Tachinidae, exhibit much longer terminal repeats, up to 381 bp [12–20]. However, data on most insect groups is very scarce compared to their species' richness. One such group is Neuroptera, a holometabolous insect order comprising about 5800 described species in 15 families [21]. Telomeres have been studied only in seven species belonging to three Neuroptera families: Myrmeleontidae, Ascalaphidae, and Chrysopidae [7,22–24]. The presence of the (TTAGG) n telomeric motif has been reported for all the studied species in two of these families—Myrmeleontidae, with three analyzed species [23], and Ascalaphidae, with two analyzed species [22,23]. In contrast, for both studied species of Chrysopidae (green lacewings)—*Chrysoperla carnea* (Stephens, 1836) [7] and *Ceraeochrysa claveri* (Navás, 1911) [24]—the absence of (TTAGG) n has been reported. The former species has been studied by Southern blotting [7], while the latter—by fluorescence in situ hybridization (FISH) [24]. Genome data for the Chrysopidae species *C. carnea* has been analyzed also using Telomeric Repeats Identification Pipeline (TRIP), a bioinformatics tool that identifies telomeric repeat motifs from Illumina short-read sequencing data by extracting and profiling 2–25 bp tandem repeats, computing 19 summary statistics including repeat-containing read counts and total repeat lengths, and ranking candidates primarily based on abundance metrics. TRIP designates a final telomeric repeat motif when a candidate shows a threshold higher abundance than other repeat units, or when this threshold is not met but additional evidence from literature or high-quality genome assemblies supports the designation. However, this pipeline did not identify any short tandem repeat telomeric motifs in the analyzed Neuroptera genome data [11].

Several noncanonical telomeric motifs have been identified in multiple insect orders, often from analyses of chromosome-level genome assemblies [25–27]. In addition, analyses of genome data, particularly in insects [28], have revealed insertions of the telomere-targeting non-LTR retrotransposons SART and TRAS into telomeric tandem-repeat regions. In such cases, telomeres comprise both telomerase-derived repeats and retrotransposon arrays [25].

However, chromosome-level assembly analyses have not been applied to Neuroptera. To our knowledge, neither noncanonical telomeric motifs nor insertions of the telomere-targeting non-LTR retrotransposons SART and TRAS have been reported in Chrysopidae.

We aimed to identify and characterize candidate telomeric motifs in Chrysopidae using chromosome-level genome assemblies, and in addition, we searched for SART/TRAS insertions.

2. Materials and Methods

Chromosome-level genome assemblies were available in GenBank for four Chrysopidae species: three Chrysopinae (*C. carnea*, *Chrysopa pallens* (Rambur, 1838), and *Nineta flava* (Scopoli, 1763)) and one Nothochrysininae (*Nothochrysa capitata* (Fabricius, 1793)), with accession numbers GCA_905475395.1, GCA_020423425.1, GCA_963920215.1, and GCA_965240235.1, respectively. We downloaded these publicly available assemblies, all of which had been generated using long-read sequencing technologies essential for accurately resolving repetitive telomeric regions that are typically problematic for short-read sequencing approaches. Specifically, *N. flava* and *N. capitata* had been assembled using

PacBio and Arima2 technologies; *C. carnea* using PacBio, Illumina, and Arima technologies; and *C. pallens*—using PacBio Sequel technology.

We applied an approach similar to that in [25–27], loading each assembly into Geneious Prime® 2025.0.3 and examining the terminal sequences through side-by-side comparison of the terminal regions of the chromosome pseudomolecules within each assembly.

Additionally, we applied five specific requirements that candidate short motifs must fulfill to qualify as optimal telomeric sequence candidates [25,26]: (1) the motifs must occupy strictly terminal locations; (2) their size should span a minimum of 300–400 bp (see [29]); (3) across a species, any candidate telomeric motif must display identical sequences in all chromosome pseudomolecules where detected; (4) within each analyzed chromosome pseudomolecule end, alternative motifs should be either absent or extremely uncommon; and (5) telomeric motifs positioned at opposite chromosome pseudomolecules’ ends must exhibit reverse-complementary organization and directionality.

To identify SART and TRAS elements in the chromosome-level genome assembly chromosome pseudomolecules in species with canonical motifs, we employed the method outlined in [25]. In this approach, the sequences “AAAAAAAAAACCTAACCTAA/TTAGGTTAGGTTTTTTTTT” and “CCTAACCTAACCTTTTTTTTTT/AAAAAAAAAAAGGTTAGGTTAGG” served as search templates for detecting retrotransposons belonging to the TRAS and SART families, respectively. The search was carried out using the “Find” tool in the graphical sequence panel (format ‘Graphics’) implemented in GenBank; the tool was used to find exact matches of the query sequences. For species exhibiting alternative motifs, the search templates were adjusted to correspond with the alternative sequence identified in each respective species.

3. Results

At the chromosome pseudomolecules’ ends of *C. carnea* and *C. pallens*, we failed to detect motifs that met all five selection criteria (listed in the Section 2) for telomeric sequences.

The best candidate for the telomeric motif in *N. flava* was the pentanucleotide (TTGGG)*n*. It occurred at the ends in five of the seven chromosome pseudomolecules. In two chromosome pseudomolecules, the motif was present at both ends; in three, it was present at only one end. In total, we identified seven terminal arrays of this repeat (Table 1). The lengths of these arrays ranged from 228 to 8005 bp (mean 4125 bp; sample standard deviation 2923 bp). Six arrays exceeded 3000 bp. In chromosome pseudomolecules OY986040.1 and OY986044.1, the pentanucleotide motifs on opposite sides of each had a reverse-complementary structure and orientation.

Table 1. Best candidate for telomeric motif in *N. flava*: occurrences of (TTGGG)*n* at the ends of the seven assembled chromosome pseudomolecules. Arrays at 5’ ends are (CCCAA)*n* (reverse complement); arrays at 3’ ends are (TTGGG)*n*.

GenBank Accession	5’	3’	Chromosome Pseudomolecules Size (bp)
OY986040.1	1–8005	150,122,476–150,126,493	150,126,493
OY986041.1	no short repeat array	142,391,635–142,396,179	142,396,181
OY986042.1	1–3300	no short repeat array	119,373,907
OY986043.1	no short repeat array	100,876,893–100,877,120	100,877,120
OY986044.1	1–7554	88,716,705–88,717,929	88,717,929
OY986045.1	no short repeat array	no short repeat array	73,119,431
OY986046.1	no short repeat array	no short repeat array	41,815,626

The best candidate for telomeric motif in *N. capitata* was the pentanucleotide (TTAGG)*n*; it was found in the ends of four chromosome pseudomolecules (out of eight) at one end of each. In total, we identified four terminal arrays of this repeat (Table 2)—three at 3' ends and one at a 5' end (reverse complement (CCTAA)*n*). Array lengths ranged from 2316 to 3808 bp (mean 2747.5 bp; sample SD 710.6 bp).

Table 2. Best candidate for telomeric motif in *N. capitata*: (TTAGG)*n*, occurrence at the ends of the eight assembled chromosome pseudomolecules. Arrays at 5' ends are (CCTAA)*n* (reverse complement); arrays at 3' ends are (TTAGG)*n*.

GenBank Accession	5'	3'	Chromosome Pseudomolecules Size (bp)
OZ251087.1	no short repeat array	123,553,250–123,555,627	123,555,627
OZ251088.1	no short repeat array	115,084,180–115,086,667	115,086,667
OZ251089.1	1–2316	no short repeat array	93,318,919
OZ251090.1	no short repeat array	no short repeat array	61,893,665
OZ251091.1	no short repeat array	54,814,880–54,818,687	54,818,687
OZ251092.1	no short repeat array	no short repeat array	53,992,875
OZ251093.1	no short repeat array	no short repeat array	8,187,640
OZ251094.1	no short repeat array	no short repeat array	24,839,040

In the chromosome-level genome assemblies of both *N. flava* and *N. capitata*, no retrotransposons from the TRAS and SART families were detected. Nucleotide variation increased internally from the chromosome termini, consistent with telomeric sequence degradation patterns.

4. Discussion

The family Chrysopidae is widespread and species-rich, with more than 1400 described species across about 80 genera and three subfamilies: Nothochrysinae, Apochrysinae, and Chrysopinae [21]. Chrysopinae are cosmopolitan (and contain ca. 97% of the species); the Apochrysinae are restricted to tropical areas in Africa, Asia, Australia, and the Americas; and the Nothochrysinae are widespread across Europe, Australia, southern Africa, South America, and western North America [30]. Owing to their predation on arthropod pests, some Chrysopidae species are used as biological control agents in diverse agroecosystems [31]. Among the species of Chrysopidae, there are predators of agricultural pests, including spider mites (Acari: Tetranychidae), whiteflies (Hemiptera: Aleyrodidae), aphids (Hemiptera: Aphididae), mealybugs (Hemiptera: Pseudococcidae), and beetles (Coleoptera) [32–34]. Despite their key role as predators of agricultural pests, Chrysopidae are understudied with respect to telomeric sequence content. We identified telomeric motifs in two Chrysopidae species for the first time: (TTAGG)*n* in *N. capitata* (Nothochrysinae) and (TTGGG)*n* in *N. flava* (Chrysopinae). While previous studies documented the absence of (TTAGG)*n* in *C. carnea* [7] and *C. claveri* [24], our findings indicate that chrysopids possess alternative telomeric sequences. Notably, the (TTGGG)*n* motif represents the first such discovery in Neuroptera, suggesting greater telomeric diversity in this order than previously recognized.

The motif TTGGG has been documented as an alternative telomeric sequence in several insect groups, including beetles (Coleoptera), where it was found in *Apoderus coryli* (Linnaeus, 1758) (Attelabidae); Odonata, in the white-legged damselfly *Platynemesis pennipes* (Pallas, 1771) (Platynemididae); and in Hymenoptera, in *Macropis europaea* Warncke, 1973 (Melittidae), where the motifs TTGGG and TTAGG are mixed, but the TTGGG motif prevailed—the TTAGG motif almost never occurs twice in a row, while TTGGG occurs in tandem arrays up to 13 repeats in length [25]. This pattern indicates that TTGGG can

functionally replace the canonical TTAGG motif in telomere maintenance. Because the TTAGG to TTGGG shift requires only a single substitution and TTGGG occurs in distantly related insect orders (Coleoptera, Odonata, Hymenoptera, and now Neuroptera), the motif has most likely arisen multiple times independently.

The phylogenetic relationships among the three Chrysopidae subfamilies remain unresolved, with different studies supporting different topologies. The earliest hypothesis, scenario (1), placed Nothochrysinæ as sister to Apochrysinæ + Chrysopinæ [30,35], but this scenario is now largely abandoned. Subsequently, nuclear and mitochondrial gene analyses supported scenario (2)—Apochrysinæ as sister to Nothochrysinæ + Chrysopinæ [36,37]. However, more recent molecular studies, including both nuclear datasets and mitochondrial genome data, have predominantly supported a different arrangement, scenario (3), where Chrysopinæ is sister to Apochrysinæ + Nothochrysinæ [38–41]. The picture becomes even more complex with anchored phylogenomics, which suggests that Nothochrysinæ may be paraphyletic rather than forming one of three distinct clades [42]. In a study using molecular supermatrix approach, the Bayesian inference suggested scenario (2), while the tree of maximum likelihood supported scenario (3) [43]. A study combining both molecular and morphological data supports scenario (2) [44].

The distribution of (TTAGG) n in Nothochrysinæ and (TTGGG) n in Chrysopinæ could be more parsimoniously explained by topologies that group these subfamilies together, such as scenario (2), with the Apochrysinæ + (Nothochrysinæ + Chrysopinæ) arrangement [36,37,44], as this would require fewer independent motif transition events. However, across insect groups, given telomeric repeat sequences occur independently in different lineages (homoplasy) [25], limiting their reliability as phylogenetically informative characters. The telomeric motif in Apochrysinæ has not yet been characterized, and we lack evidence that repeat sequences are conserved within Chrysopidae lineages. Therefore, using current telomere data to distinguish among competing hypotheses of subfamily relationships would be premature. Broader taxonomic sampling across Chrysopidae, combined with independent verification methods such as fluorescence in situ hybridization (FISH) or long-read sequencing of chromosome termini, is needed to establish whether specific repeat motifs are consistently maintained within clades. Only after clade-specific conservation has been demonstrated should the observed telomeric sequences—(TTAGG) n in Nothochrysinæ and (TTGGG) n in Chrysopinæ species—be used to evaluate alternative phylogenetic trees based on the principle of minimizing evolutionary changes.

In most eukaryotes, a ribonucleoprotein reverse transcriptase enzyme (telomerase) is involved in telomere length maintenance. This specialized reverse transcriptase (TERT) uses an internal RNA template molecule (TR) to add short, simple repeats to chromosome ends [45]. Telomerase RNA (TR) has been scarcely studied in insects. The main exception is Hymenoptera, where a comprehensive study showed a switch to plant/ciliate-like TR biogenesis [16], which contrasts with TRs in other animals and fungi. The hymenopteran TR has multiple stem-loops positioned 3' of the template and 5' of the pseudoknot, which may help explain the unusual diversity of telomeric repeats reported in this order [11,25]. A similar mechanism may operate in Chrysopidae, potentially accounting for the reported telomeric sequence diversity in the family. This can be tested by studies on TRs across Chrysopidae using the approach applied by Fajkus et al. [16]. A similar notion has been previously inferred for the telomeric sequence diversity in Heteroptera [46].

The telomeric motifs identified here can be used for developing additional fluorescence in situ hybridization (FISH) probes to study/understand chromosomal organization, karyotype evolution, and genome stability in green lacewings.

5. Conclusions

The occurrence of (TTAGG)*n* in *N. capitata* contrasts with the reported absence of this motif in other Chrysopidae. The discovery of (TTGGG)*n* in *N. flava* represents the first documentation of this alternative pentanucleotide motif in Neuroptera, expanding the known telomeric sequence diversity within the order. The coexistence of both ancestral and alternative telomeric motifs in Chrysopidae suggests that other Neuroptera families may also harbor diverse telomeric sequences, indicating that broader surveys across the order are needed.

Author Contributions: Conceptualization, D.S.; methodology, D.S.; software, D.S.; validation, D.S. and S.G.; formal analysis, D.S.; investigation, D.S.; resources, D.S.; data curation, D.S. and S.G.; writing—original draft preparation, D.S.; writing—review and editing, D.S. and S.G.; All authors have read and agreed to the published version of the manuscript.

Funding: We used shared computational access provided through the project “The Evolutionary Role of the South-Eastern European Mountain System (SEEMS) as a Center of Speciation, Dispersal, and Refugium for European Terrestrial Invertebrates and its Conservation Importance as a Biodiversity Hotspot”, funded by the National Science Fund, Ministry of Education, Youth and Science of the Republic of Bulgaria under the “Vihren” program, Grant KII-06-ДБ/4 from 16.12.2024.

Institutional Review Board Statement: Not applicable. Ethical review and approval were waived because the study used only publicly available genomic datasets and involved no animals, tissues, or field sampling.

Informed Consent Statement: Not applicable.

Data Availability Statement: The original contributions presented in this study are included in the article. Further inquiries can be directed at the corresponding author.

Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

References

1. Pisano, S.; Galati, A.; Cacchione, S. Telomeric nucleosomes: Forgotten players at chromosome ends. *Cell. Mol. Life Sci.* **2008**, *65*, 3553–3563. [[CrossRef](#)]
2. O’Sullivan, R.J.; Karlseder, J. Telomeres: Protecting chromosomes against genome instability. *Nat. Rev. Mol. Cell Biol.* **2010**, *11*, 171–181. [[CrossRef](#)]
3. Galati, A.; Micheli, E.; Cacchione, S. Chromatin structure in telomere dynamics. *Front. Oncol.* **2013**, *3*, 46. [[CrossRef](#)]
4. Lazzerini-Denchi, E.; Sfeir, A. Stop pulling my strings—What telomeres taught us about the DNA damage response. *Nat. Rev. Mol. Cell Biol.* **2016**, *17*, 364–378. [[CrossRef](#)]
5. Zakian, V.A. Telomeres: Beginning to understand the end. *Science* **1995**, *270*, 1601–1607. [[CrossRef](#)]
6. Vicari, M.R.; Bruschi, D.P.; Cabral-de-Mello, D.C.; Nogaroto, V. Telomere organization and the interstitial telomeric sites involvement in insects and vertebrates chromosome evolution. *Genet. Mol. Biol.* **2022**, *45*, e20220071. [[CrossRef](#)] [[PubMed](#)]
7. Frydrychová, R.; Grossmann, P.; Trubač, P.; Vítková, M.; Marec, F. Phylogenetic distribution of TTAGG telomeric repeats in insects. *Genome* **2004**, *47*, 163–178. [[CrossRef](#)] [[PubMed](#)]
8. Vítková, M.; Král, J.; Traut, W.; Zrzavý, J.; Marec, F. The evolutionary origin of insect telomeric repeats, (TTAGG)*n*. *Chromosome Res.* **2005**, *13*, 145–156. [[CrossRef](#)] [[PubMed](#)]
9. Lukhtanov, V.A.; Kuznetsova, V.G. What genes and chromosomes say about the origin and evolution of insects and other arthropods? *Russ. J. Genet.* **2010**, *46*, 1115–1121. [[CrossRef](#)]
10. Kuznetsova, V.; Grozeva, S.; Gokhman, V. Telomere structure in insects: A review. *J. Zool. Syst. Evol. Res.* **2020**, *58*, 127–158. [[CrossRef](#)]
11. Zhou, Y.; Wang, Y.; Xiong, X.; Appel, A.G.; Zhang, C.; Wang, X. Profiles of telomeric repeats in Insecta reveal diverse forms of telomeric motifs in Hymenopterans. *Life Sci. Alliance* **2022**, *5*, e202101163. [[CrossRef](#)]
12. Gokhman, V.E.; Kuznetsova, V.G. Presence of the canonical TTAGG insect telomeric repeat in the Tenthredinidae (Symphyta) suggests its ancestral nature in the order Hymenoptera. *Genetica* **2018**, *146*, 341–344. [[CrossRef](#)] [[PubMed](#)]

13. Grozeva, S.; Anokhin, B.A.; Simov, N.; Kuznetsova, V.G. New evidence for the presence of the telomeric motif (TTAGG)*n* in the family Reduviidae and its absence in the families Nabidae and Miridae (Hemiptera, Cimicomorpha). *Comp. Cytogenet.* **2019**, *13*, 283–295. [[CrossRef](#)] [[PubMed](#)]
14. Prušáková, D.; Peska, V.; Pekár, S.; Bubeník, M.; Čížek, L.; Bezděk, A.; Čapková Frydrychová, R. Telomeric DNA sequences in beetle taxa vary with species richness. *Sci. Rep.* **2021**, *11*, 13319. [[CrossRef](#)] [[PubMed](#)]
15. Lukhtanov, V.A. Diversity and evolution of telomere and subtelomere DNA sequences in insects. *bioRxiv* **2022**. [[CrossRef](#)]
16. Fajkus, P.; Adámik, M.; Nelson, A.D.L.; Kilar, A.M.; Franek, M.; Bubeník, M.; Frydrychová, R.Č.; Votavová, A.; Sýkorová, E.; Fajkus, J.; et al. Telomerase RNA in Hymenoptera (Insecta) switched to plant/ciliate-like biogenesis. *Nucleic Acids Res.* **2023**, *51*, 420–433. [[CrossRef](#)]
17. Lyčka, M.; Bubeník, M.; Závodník, M.; Peska, V.; Fajkus, P.; Demko, M.; Fajkus, J.; Fojtová, M. TeloBase: A community-curated database of telomere sequences across the tree of life. *Nucleic Acids Res.* **2024**, *52*, D311–D321. [[CrossRef](#)]
18. Stoianova, D.; Grozeva, S.; Golub, N.V.; Anokhin, B.A.; Kuznetsova, V.G. The first FISH confirmed non-canonical telomeric motif in Heteroptera: *Cimex lectularius* Linnaeus, 1758 and *C. hemipterus* (Fabricius, 1803) (Hemiptera, Cimicidae) have a 10 bp motif (TTAGGGATGG)*n*. *Genes* **2024**, *15*, 1026. [[CrossRef](#)]
19. Bugrov, A.; Karamysheva, T.; Buleu, O. New insights into the chromosomes of stoneflies: I. Karyotype, C-banding and localization of ribosomal and telomeric DNA markers in *Skwala compacta* (McLachlan, 1872) (Polyneoptera, Plecoptera, Perlodidae) from Siberia. *Comp. Cytogenet.* **2024**, *18*, 15–26. [[CrossRef](#)]
20. Golub, N.; Anokhin, B.; Kuznetsova, V. Non-canonical telomeric motif TTAGGGGTGG in the true bug species *Geocoris dispar* Waga, 1839 (Heteroptera, Geocoridae). *Comp. Cytogenet.* **2025**, *19*, 117–123. [[CrossRef](#)]
21. Oswald, J.D.; Machado, R.J.P. Biodiversity of the Neuropterida (Insecta: Neuroptera: Megaloptera, and Raphidioptera). In *Insect Biodiversity: Science and Society*, 2nd ed.; Footitt, R.G., Adler, P.H., Eds.; John Wiley & Sons: Oxford, UK, 2018; Volume 2, pp. 627–671.
22. Okazaki, S.; Tsuchida, K.; Maekawa, H.; Ishikawa, H.; Fujiwara, H. Identification of a pentanucleotide telomeric sequence, (TTAGG)*n*, in the silkworm *Bombyx mori* and in other insects. *Mol. Cell. Biol.* **1993**, *13*, 1424–1432.
23. Kuznetsova, V.G.; Khabiev, G.N.; Anokhin, B.A. Cytogenetic study on antlions (Neuroptera, Myrmeleontidae): First data on telomere structure and rDNA location. *Comp. Cytogenet.* **2016**, *10*, 647–656. [[CrossRef](#)]
24. Cabral-de-Mello, D.C.; Gasparotto, A.E.; Rico-Porras, J.M.; Ferretti, A.B.S.; Mora-Ruiz, P.; Alves-Gomes, R.T.; Lourejan, V.; Scudeler, E.L.; Lorite, P.; Bardella, V.B. First insights into the satellitomes and new evidence for the absence of canonical insect telomere in the Neuroptera order. *Genome* **2025**, *68*, 1–12. [[CrossRef](#)]
25. Lukhtanov, V.A.; Pazhenkova, E.A. Diversity and evolution of telomeric motifs and telomere DNA organization in insects. *Biol. J. Linn. Soc.* **2023**, *140*, 536–555. [[CrossRef](#)]
26. Lukhtanov, V.A. Telomere DNA in the insect order Dermaptera and the first evidence for the non-canonical telomeric motif TTCGG in Arthropoda. *Comp. Cytogenet.* **2025**, *19*, 13–18. [[CrossRef](#)] [[PubMed](#)]
27. Kuznetsova, V.; Golub, N.; Anokhin, B.; Stoianova, D.; Lukhtanov, V. Diversity of telomeric sequences in true bugs (Heteroptera): New data on the infraorders Pentatomomorpha and Cimicomorpha. *Cytogenet. Genome Res.* **2025**, 192–205. [[CrossRef](#)] [[PubMed](#)]
28. Kubo, Y.; Okazaki, S.; Anzai, T.; Fujiwara, H. Structural and phylogenetic analysis of TRAS, telomeric repeat-specific non-LTR retrotransposon families in lepidopteran insects. *Mol. Biol. Evol.* **2001**, *18*, 848–857. [[CrossRef](#)]
29. Watson, J.M.; Trieb, J.; Troestl, M.; Renfrew, K.; Mandáková, T.; Fulneček, J.; Shippen, D.E.; Říha, K. A hypomorphic allele of telomerase uncovers the minimal functional length of telomeres in Arabidopsis. *Genetics* **2021**, *219*, iyab126. [[CrossRef](#)]
30. Brooks, S.J.; Barnard, P.C. The green lacewings of the world: A generic review (Neuroptera: Chrysopidae). *Bull. Br. Mus. Nat. Hist. Entomol.* **1990**, *59*, 117–286.
31. Pappas, M.L.; Broufas, G.D.; Tsarsitalidou, O.K.; Koveos, D.S. Development and reproduction of the lacewings *Dichochrysa flavifrons* and *Dichochrysa zelleri* (Neuroptera: Chrysopidae) fed on two prey species. *Ann. Entomol. Soc. Am.* **2011**, *104*, 726–732. [[CrossRef](#)]
32. Sablon, L.; Haubruge, E.; Verhegeen, F.J. Consumption of immature stages of Colorado potato beetle by *Chrysoperla carnea* (Neuroptera: Chrysopidae) larvae in the laboratory. *Am. J. Potato Res.* **2013**, *90*, 51–57. [[CrossRef](#)]
33. Alghamdi, A.; Al-Otaibi, S.; Sayed, S.M. Field evaluation of indigenous predacious insect, *Chrysoperla carnea* (Steph.) (Neuroptera: Chrysopidae), fitness in controlling aphids and whiteflies in two vegetable crops. *Egypt. J. Biol. Pest Control* **2018**, *28*, 20. [[CrossRef](#)]
34. Silva, C. Prey Preference of *Chrysoperla rufilabris* (Burmeister) (Neuroptera: Chrysopidae) For Three Common Pest Species of Greenhouse Crops. Master's Thesis, Clemson University, Clemson, SC, USA, 2023.
35. Brooks, S.J. An overview of the current status of Chrysopidae (Neuroptera) systematics. *Dtsch. Entomol. Z.* **1997**, *44*, 267–275. [[CrossRef](#)]
36. Winterton, S.L.; De Freitas, S. Molecular phylogeny of the green lacewings (Neuroptera: Chrysopidae). *Aust. J. Entomol.* **2006**, *45*, 235–243. [[CrossRef](#)]

37. Dai, L.; Winterton, S.L.; Garzón-Orduña, I.J.; Liang, F.Y.; Liu, X.Y. Mitochondrial phylogenomic analysis resolves the subfamily placement of enigmatic green lacewing genus *Nothancyla* (Neuroptera: Chrysopidae). *Austral. Entomol.* **2017**, *56*, 322–331. [[CrossRef](#)]
38. Haruyama, N.; Mochizuki, A.; Duelli, P.; Naka, H.; Nomura, M. Green lacewing phylogeny, based on three nuclear genes (Chrysopidae, Neuroptera). *Syst. Entomol.* **2008**, *33*, 275–288. [[CrossRef](#)]
39. Duelli, P.; Henry, C.S.; Mochizuki, A. The endemic *Atlantochrysa atlantica* (McLachlan) (Neuroptera: Chrysopidae) on Atlantic Islands: African or American origin? *J. Nat. Hist.* **2014**, *48*, 2595–2608. [[CrossRef](#)]
40. Jiang, Y.; Garzón-Orduña, I.J.; Winterton, S.L.; Yang, F.; Liu, X. Phylogenetic relationships among tribes of the green lacewing subfamily Chrysopinae recovered based on mitochondrial phylogenomics. *Sci. Rep.* **2017**, *7*, 7218.
41. Tian, S.; Jiang, Y.; Lai, Y.; Wang, S.; Liu, X.; Wang, Y. New mitogenomes of the green lacewing tribe Ankylopterygini (Neuroptera: Chrysopidae: Chrysopinae) and phylogenetic implications of Chrysopidae. *Insects* **2023**, *14*, 878. [[CrossRef](#)]
42. Winterton, S.L.; Gillung, J.P.; Garzón-Orduña, I.J.; Badano, D.; Breitkreuz, L.C.; Duelli, P.; Engel, M.S.; Liu, X.; Machado, R.J.; Mansell, M.; et al. Evolution of green lacewings (Neuroptera: Chrysopidae): An anchored phylogenomics approach. *Syst. Entomol.* **2019**, *44*, 514–526. [[CrossRef](#)]
43. Garzón-Orduña, I.J.; Winterton, S.L.; Jiang, Y.; Breitkreuz, L.C.V.; Duelli, P.; Engel, M.S.; Penny, N.D.; Tauber, C.A.; Mochizuki, A.; Liu, X. Evolution of green lacewings (Neuroptera: Chrysopidae): A molecular supermatrix approach. *Syst. Entomol.* **2019**, *44*, 499–513. [[CrossRef](#)]
44. Breitkreuz, L.C.V.; Garzón-Orduña, I.J.; Winterton, S.L.; Engel, M.S. Phylogeny of Chrysopidae (Neuroptera), with emphasis on morphological trait evolution. *Zool. J. Linn. Soc.* **2022**, *194*, 1374–1395. [[CrossRef](#)]
45. Greider, C.W.; Blackburn, E.H. A telomeric sequence in the RNA of *Tetrahymena* telomerase required for telomere repeat synthesis. *Nature* **1989**, *337*, 331–337. [[CrossRef](#)] [[PubMed](#)]
46. Stoianova, D.; Grozeva, S.; Todorova, N.; Rangelov, M.; Lukhtanov, V.A.; Kuznetsova, V.G. New Insights into the Telomere Structure in Hemiptera (Insecta) Inferred from Chromosome-Level and Scaffold-Level Genome Assemblies. *Diversity* **2025**, *17*, 552. [[CrossRef](#)]

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.