HETeroptera POLONIAE
ACTA FAUNISTICA 19

Heteroptera Poloniae – Acta Faunistica
vol. 19: 79–86. Opole, 8 XII 2025
ISSN 2083-201X
http://doi.org/10.5281/zenodo.17807250

Review article

5S rRNA in Heteroptera – the current state of knowledge and future prospects

JERZY A. LIS *, KAMILA GOLONKA

Institute of Biology, University of Opole, Oleska 22, 45-052 Opole, Poland
** corresponding author: cydnus@uni.opole.pl*

Abstract. This paper provides a comprehensive overview of current research on 5S rRNA in true bugs (Heteroptera). It also highlights existing findings and potential possibilities for future investigation in this field.

Key words: Hemiptera, Cimicomorpha, Pentatomomorpha, ribosomal RNA, RNA secondary structure, RNA tertiary structure, molecular marker, phylogeny.

Introduction

Ribosomal RNAs, as components of eukaryotic ribosomes, are essential for protein synthesis and consist of four types: 5S rRNA, 18S rRNA, 5.8S rRNA, and 28S rRNA (e.g., Dinman 2009; Taylor et al. 2009; Ramakrishnan 2011; Wilson & Doudna Cate 2012; Anger et al. 2013; Gokhman & Kuznetsova 2024).

The smallest among these five structures is 5S rRNA (about 120 nucleotides), and it is the least frequently used element of ribosomal RNA in phylogenetic analyses because it is considered highly conserved across all eukaryotes (Szymański et al. 2003; Ciganda & Williams 2011; Vierna et al. 2013). Its secondary and tertiary structures have also rarely been analysed and predicted (McDougall & Nazar 1983; Ciganda & Williams 2011).

In true bugs (Hemiptera: Heteroptera), the most common ribosomal RNAs to be included in this type of analysis were 18S rRNA and 28S rRNA (Ouvrard et al. 2000; Li H.M. et al. 2005, 2006; Xie et al. 2005, 2008; Grazia et al. 2008; Li M. et al. 2012; Yu et al. 2013; Song et al. 2016; Wang et al. 2016; Wu et al. 2016, 2018; Lis J.A. et al. 2017; Weirauch et al. 2019; Bianchi et al. 2021; Roca-Cusachs et al. 2022; Lis B. et al. 2023; Lis J.A. 2023; Lis J.A. & Domagała 2024).

Although data for 5S rRNA (5S rDNA) have been published for various insect groups (Gillespie et al. 2006; Cabral-de-Mello 2011a, 2011b; Bueno et al. 2016; Volarić et al. 2024; Taha 2025), only one study referenced this gene in Heteroptera (Bardella & Cabral-de-Mello 2018). Sequences of the 5S rDNA were obtained for two species of the family Coreidae and deposited in GenBank (Bardella & Cabral-de-Mello 2018). Furthermore, we found that many 5S rRNA sequences for Hemiptera are also available in GenBank and other online databases, despite the lack of formal publications concerning these sequences.

For example, the RNACentral database (https://rnacentral.org) contains 3,064 5S rRNA sequences for Hemiptera, of which only 264 are sequences for Heteroptera.

Therefore, we have decided to summarise all data related to 5S rRNA (5S rDNA) in Heteroptera and to propose further research involving the 5S rDNA gene sequence and the structures of the ribosomal RNA (5S rRNA) encoded by it. All information was obtained from three databases: RNACentral (http://rnacentral.org), the 5S RNA Database (http://combio.pl/rrna/), and GenBank (https://www.ncbi.nlm.nih.gov).

The following list specifies, for each of the ten recorded Heteroptera species, their classification, the number of sequences available in each database, the lengths of these sequences, the presence of secondary structure information, and the prediction method used (where available within the respective database).

A list of species

Infraorder: Cimicomorpha

Family: Reduviidae

***Rhodnius prolixus* Stål, 1859**

RNA Central Database

Total: 49 sequences; reference genomes: 47 sequences.

Number of nucleotides (number of sequences): 126 (1); 122 (4); 121 (3); 120 (6); 119 (23); 118 (1); 117 (3); 115 (2); 114 (1); 110 (1); 108 (2); 107 (1); 103 (1).

Secondary structure available: 46 sequences.

Secondary structure prediction: R2DT software.

5S RNA Database

No data.

GenBank

Total: 42 sequences (predicted).

Number of nucleotides (number of sequences): 122 (1); 121 (2); 120 (2); 119 (37).

Secondary structure: not available.

Family: Cimicidae

***Cimex lectularius* Linnaeus, 1758**

RNA Central Database

Total: 21 sequences; reference genomes: 19 sequences.

Number of nucleotides (number of sequences): 122 (3); 119 (11); 117 (1); 115 (2); 113 (1); 111 (1); 103 (2).

Secondary structure available: 20 sequences.

Secondary structure prediction: R2DT software.

5S RNA Database

Total: 3 sequences.

Number of nucleotides (number of sequences): 122 (3).

Secondary structure available: 3 sequences.

GenBank

Total: 10 sequences (predicted).

Number of nucleotides (number of sequences): 119 (10).

Secondary structure: not available.

Family: Miridae

***Apolygus lucorum* (Meyer-Dür, 1843)**

RNA Central Database

Total: 95 sequences; reference genomes: none.

Number of nucleotides (number of sequences): 131 (1); 129 (1); 123 (3); 121 (2); 120 (6); 119 (39); 118 (12); 117 (2); 116 (3); 115 (2); 114 (2); 113 (1); 112 (1) 111 (2); 110 (2); 108 (2); 106 (3); 105 (2); 103 (1); 102 (2); 99 (1); 95 (1); 92 (1); 88 (1); 81 (1); 76 (1).

Secondary structure: not available.

5S RNA Database

No data.

GenBank

No data.

***Nesidiocoris tenuis* (Reuter, 1895)**

RNA Central Database

Total: 8 sequences; reference genomes: none.

Number of nucleotides (number of sequences): 119 (6); 82 (1); 75 (1).

Secondary structure: not available.

5S RNA Database

No data.

GenBank

No data.

Infraorder: Pentatomomorpha

Family: Lygaeidae

***Oncopeltus fasciatus* (Dallas, 1852)**

RNA Central Database

Total: 10 sequences; reference genomes: none.

Number of nucleotides (number of sequences): 122 (10)

Secondary structure available: 10 sequences.

Secondary structure prediction: R2DT software.

5S RNA Database

Total: 10 sequences.

Number of nucleotides (number of sequences): 122 (10).

Secondary structure available: 10 sequences.

GenBank

No data.

Family: Pentatomidae

***Halyomorpha halys* (Stål, 1855)**

RNA Central Database

Total: 3 sequences; reference genomes: 3 sequences.

Number of nucleotides (number of sequences): 119 (3).

Secondary structure available: 3 sequences.

Secondary structure prediction: R2DT software.

5S RNA Database

No data.

GenBank

Total: 4 sequences (predicted).

Number of nucleotides (number of sequences): 119 (4).

Secondary structure: not available.

***Nezara viridula* (Linnaeus, 1758)**

RNA Central Database

Total: 30 sequences; reference genomes: none.

Number of nucleotides (number of sequences): 142 (1); 128 (1); 123 (1); 122 (2); 121 (1); 120 (4); 119 (15); 118 (2); 114 (1); 113 (1); 99 (1).

Secondary structure available: 1 sequence (119 nucleotides).

Secondary structure prediction: R2DT software.

5S RNA Database

No data.

GenBank

No data.

***Piezodorus guildinii* (Westwood, 1837)**

RNA Central Database

Total: 1 sequence; reference genomes: none.

Number of nucleotides (number of sequences): 122 (1).

Secondary structure available: 1 sequence.

Secondary structure prediction: R2DT software.

5S RNA Database

Total: 1 sequence.

Number of nucleotides (number of sequences): 122 (1).

Secondary structure available: 1 sequence.

GenBank

No data.

Family: Coreidae

***Chariesterus armatus* (Thunberg, 1825)**

RNA Central Database

No data

5S RNA Database

No data

GenBank

Total: 6 sequences.

Number of nucleotides (number of sequences): 256 (1); 246 (1); 192 (1); 187 (1); 179 (1); 170 (1).

Note: Sequences of this species were published (Bardella & Cabral-de-Mello, 2018). However, each complete sequence includes 5S ribosomal RNA and the non-transcribed spacer (NTS).

***Holhymenia histrio* (Fabricius, 1803)**

RNA Central Database

No data

5S RNA Database

No data

GenBank

Total: 5 sequences.

Number of nucleotides (number of sequences): 1168 (1); 849 (1); 735 (1); 703 (1); 666 (1).

Note: Sequences of this species were published (Bardella & Cabral-de-Mello, 2018). However, each complete sequence includes 5S ribosomal RNA and the non-transcribed spacer (NTS).

5S rRNA secondary structures prediction

In the analysed databases, information on the programme (R2DT; Sweeney et al., 2021) used to predict the secondary structure of 5S rRNA was available only in the RNACentral database (The RNAcentral Consortium, 2019).

Secondary structures for some sequences are also provided in the 5S RNA Database (Szymanski et al., 2016). In this case, each record included data on the secondary structure, displayed as a diagram. Detailed information on the creation of these secondary structures is available in the 5S RNA Database under the 'Help' tab (refer to: '5S rRNA gene record' and 'Alignment').

The diagrams in Figure 1 (Fig. 1) illustrate the secondary structures of the 5S rRNA from the *Piezodorus guildinii* sequence (as an example) in both the RNACentral database and the 5S RNA Database. Additionally, we present (Fig. 2) the same sequence as secondary structures generated using RNAstructure version 6.3 (Reuter & Mathews 2010). This programme has been successfully used many times to predict secondary structures of rRNA in Heteroptera (Lis B. et al. 2023; Lis J.A. 2023; Lis J.A. & Domagała 2024).

5S rRNA tertiary structures prediction

Unfortunately, unlike the secondary structures of 5S rRNA, the tertiary structures of this ribosomal RNA have never been predicted in Heteroptera. Such data are absent from any publication or database.

Therefore, in this paper, we present the tertiary structures of the 5S rRNA from two species, *Piezodorus guildini* and *Nezara viridula*, as examples (Fig. 3). The predictions were made using RNAComposer (http://rnacomposer.ibch.poznan.pl/), a fully automated, accurate, and precise RNA structure modelling server (Popenda et al. 2012; Biesiada et al. 2016; Kulkarni et al. 2023). The tertiary structure images were visualised using PyMol software version 2.4.0 (Schrodinger & DeLano 2020).

For comparison, we have also included a model of the tertiary structure of 5S rRNA from the halophilic archaeon *Haloarcula marismortui* (Volcani, 1940) (Oren et al. 1990; Fig. 3D). This is currently the most well-known model of 5S rRNA tertiary structure (Ban et al. 2000; Sun & Caetano-Anollés 2009).

Conclusions and future perspectives

1. Although 5S rRNA has been studied for decades, many questions about its secondary and tertiary structures remain unresolved.

2. This is especially significant for insects, particularly those in the suborder Heteroptera within the order Hemiptera.

3. A comparison of the number of 5S rRNA sequences available in databases and publications for the entire order Hemiptera and the suborder Heteroptera indi-

cates that further research into the 5S rRNA sequences of Heteroptera species is necessary.

4. Analysing the secondary and tertiary structures of 5S rRNA should include as many taxa as possible to detect differences at the species, genus, family, superfamily, and infraorder levels.

5. These analyses may assist in assessing the importance of 5S rRNA as a molecular marker in phylogenetic research on Hemiptera, particularly Heteroptera, across various taxonomic levels.

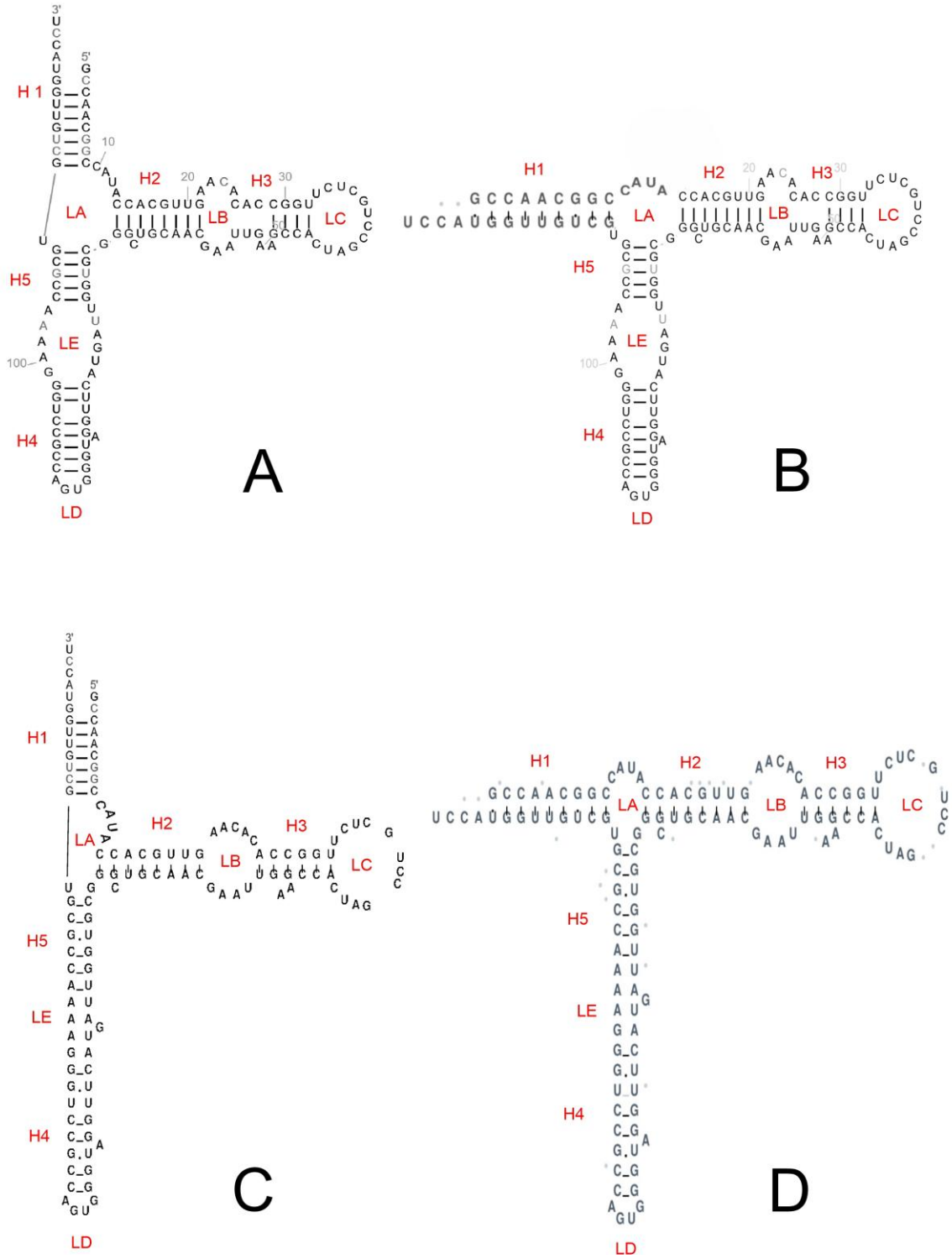

Fig. 1. Secondary structures of the 5S rRNA from the *Piezodorus guildinii* sequence in the RNACentral database (A–B) and the 5S RNA DB (C–D). The structures in B and C have been modified accordingly (B – according to the scheme used in the RNACentral database; C – according to the scheme used in the 5S RNA DB). Nomenclature of loops (LA, LB, LC, LD, LE) and helices (H1, H2, H3, H4, H5) follow Szymański et al. (2003).

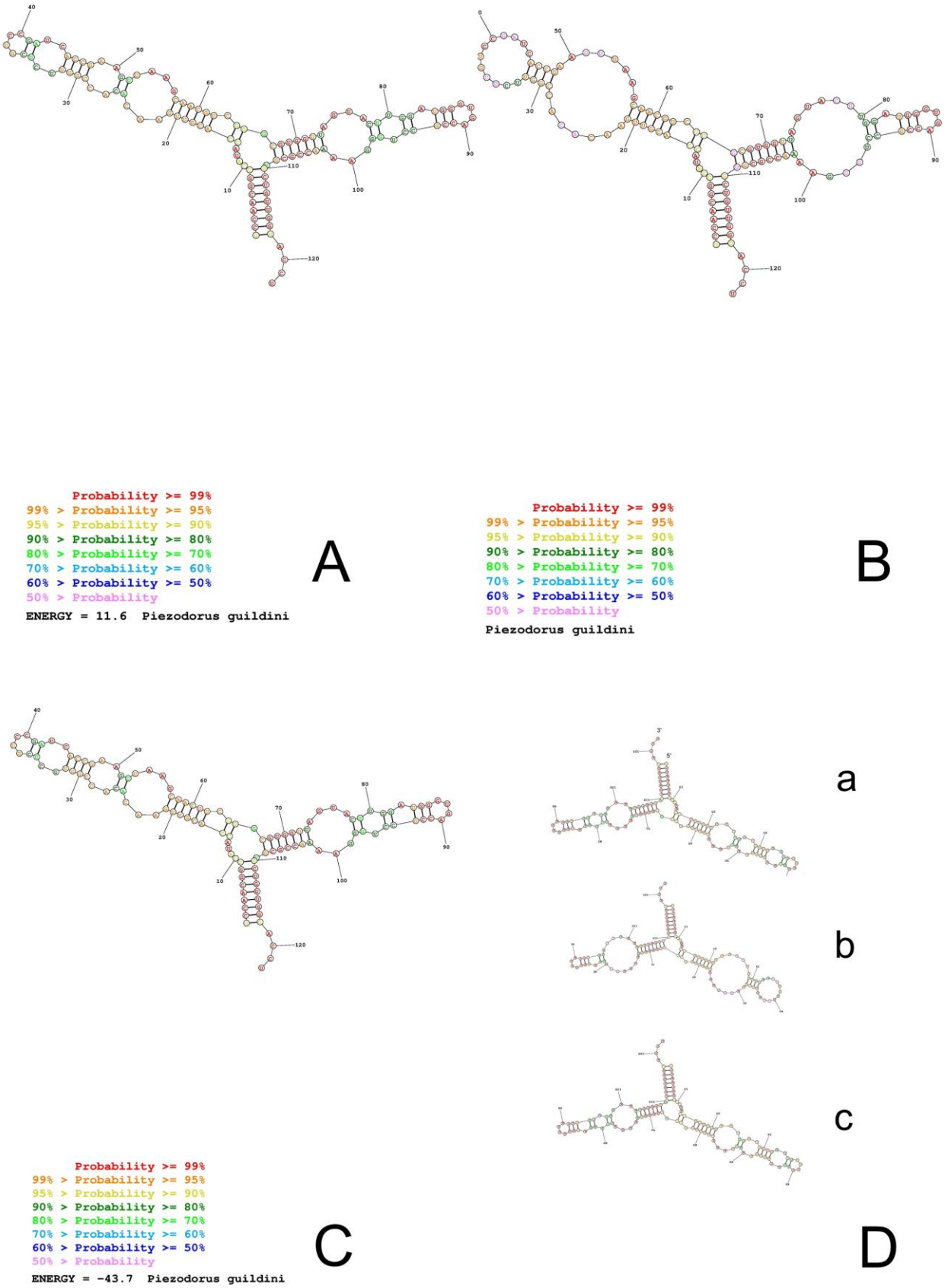

Fig. 2. Secondary structures of the 5S rRNA from the *Piezodorus guildinii* sequence generated by RNAstructure ver. 6.3. A. predicted MaxExpect structure. B. predicted ProbKnot structure. C. predicted lowest free energy structure. D. comparison of all three structures predicted by RNAstructure ver. 6.3. The labels [a, b, c] correspond to the structures labelled A, B and C, respectively. The structures in figure D have been rotated according to the scheme presented in Sun & Caetano-Anollés (2009).

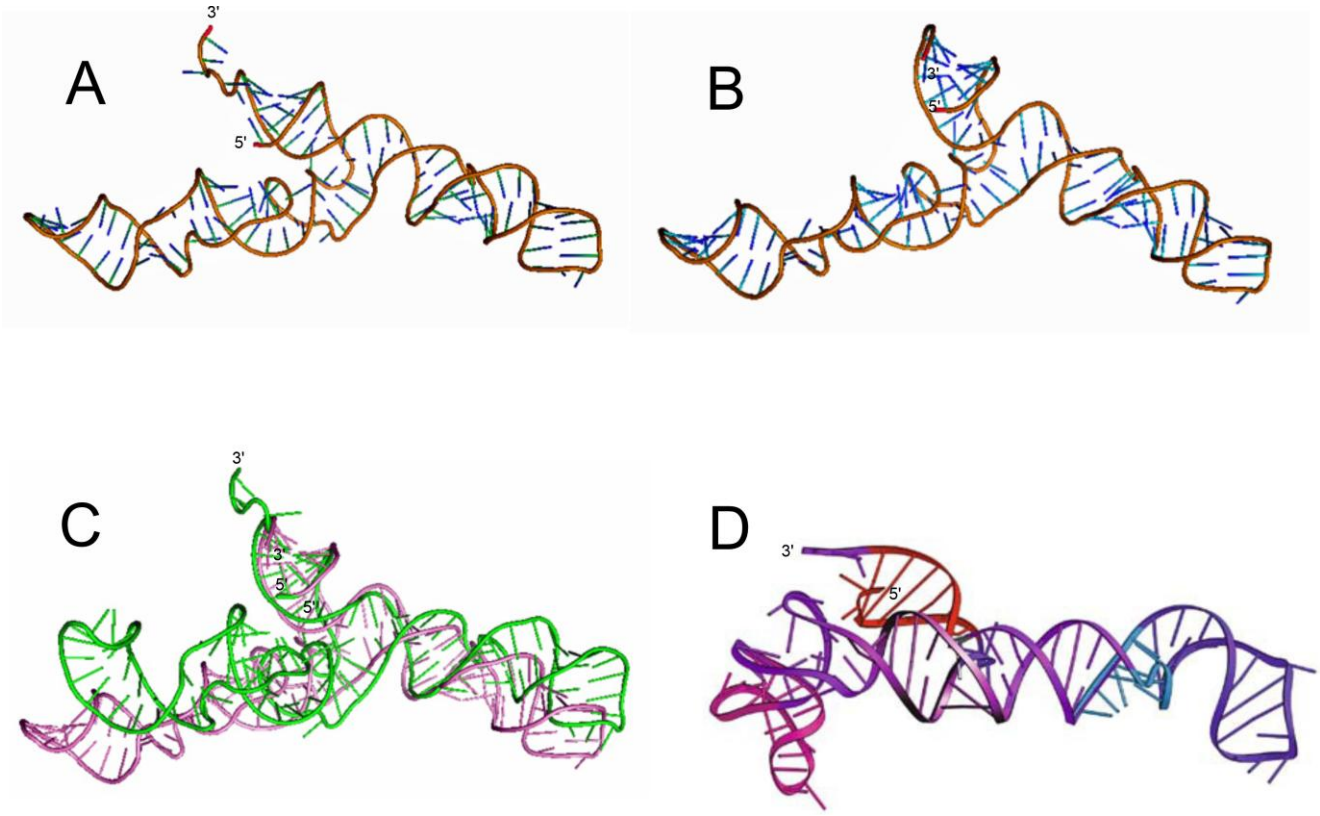

Fig. 3. Tertiary structures of the 5S rRNA. A. *Piezodorus guildini*. B. *Nezara viridula*. C. *Piezodorus guildini* and *Nezara viridula* in the same position, compared using PyMol (green – *Piezodorus guildini*, pink – *Nezara viridula*). D. halophilic archaeon *Haloarcula marismortui*.

References

Anger A., Armache J.P., Berninghausen O., Habeck, M., Subklewe M., Wilson D.N., Beckmann R. 2013. Structures of the human and *Drosophila* 80S ribosome. *Nature* **497**: 80–85. https://doi.org/10.1038/nature12104

Ban N., Nissen P., Hansen J., Moore P.B., Steitz T.A. 2000. The complete atomic structure of the large ribosomal subunit at 2.4 A° resolution. *Science* **289**: 905–920. https://doi.org/10.1126/science.289.5481.905

Bardella V.B., Cabral-de-Mello D.C. 2018. Uncovering the molecular organization of unusual highly scattered 5S rDNA: The case of *Chariesterus armatus* (Heteroptera). *Gene* **646**: 153–158. https://doi.org/10.1016/j.gene.2017.12.030

Biesiada M., Purzycka K.J., Szachniuk M., Blazewicz J., Adamiak R.W. 2016. Automated RNA 3D structure prediction with RNAComposer. [in:] Turner D., Mathews D., (eds.) *RNA Structure Determination: Methods in Molecular Biology*. Humana Press, New York, NY, USA, 1490, 199–215.

Bianchi F.M., Barão K.R., Grassi A., Ferrari A. 2021. A milestone for Pentatomoidea: Grazia et al. 2008- What do we know and where can we go? *Zootaxa* **4958**: 406–429. https://doi.org/10.11646/zootaxa.4958.1.26

Bueno D., Palacios-Gimenez O.M., Martí D.A., Mariguela T.C., Cabral-de-Mello D.C. 2016. The 5S rDNA in two Abracris grasshoppers (Ommatolampidinae: Acrididae): molecular and chromosomal organization. *Molecular genetics and genomics*, **291(4)**: 1607–1613. https://doi.org/10.1007/s00438-016-1204-1

Cabral-de-Mello D.C., Oliveira S., Moura R.C., Martins C. 2011a. Chromosomal organization of the 18S and 5S rRNAs and histone H3 genes in Scarabaeinae coleopterans: insights into the evolutionary dynamics of multigene families and heterochromatin. *BMC Genetics* **12**: 88.

Cabral-de-Mello D.C., Cabrero J., López-León M.D., Camacho J.P.M., 2011b. Evolutionary dynamics of 5S rDNA location in acridid grasshoppers and its relationship with histone gene and 45S rDNA location. *Genetica* **139**: 921–931.

Ciganda M., Williams N. 2011. Eukaryotic 5S rRNA biogenesis. *Wiley interdisciplinary reviews. RNA*, **2(4)**: 523–533. https://doi.org/10.1002/wrna.74

Dinman J. D. 2009. The eukaryotic ribosome: current status and challenges. *Journal of Biological Chemistry* **284(18):** 11761–11765.

Gillespie J.J., Johnston J.S., Cannone J.J., Gutell R.R. 2006. Characteristics of the nuclear (18S, 5.8S, 28S and 5S) and mitochondrial (12S and 16S) rRNA genes of *Apis mellifera* (Insecta: Hymenoptera): structure, organization, and retrotransposable elements. *Insect Molecular Biology* **15(5)**: 657–686.

Gokhman V.E., Kuznetsova V.G. 2024. Structure and Evolution of Ribosomal Genes of Insect Chromosomes. *Insects* **15(8)**: 593. https://doi.org/10.3390/insects15080593

Grazia J., Schuh R.T., Wheeler W.C. 2008. Phylogenetic relationships of family groups in Pentatomoidea based on morphology and DNA sequences (Insecta: Heteroptera). *Cladistics* **24**: 932–976. https://doi.org/10.1111/j.1096-0031.2008.00224.x

Kulkarni M., Thangappan J., Deb I., Wu S. 2023. Comparative analysis of RNA secondary structure accuracy on predicted RNA 3D models. *PLoS ONE* **18(9)**: e0290907. https://doi.org/10.1371/journal.pone.0290907

Li H.M., Deng R.Q., Wang J.W., Chen Z.Y., Jia F.L., Wang X.Z. 2005. A preliminary phylogeny of the Pentatomomorpha (Hemiptera: Heteroptera) based on nuclear 18S rDNA and mitochondrial DNA sequences. *Molecular Phylogenetics & Evolution* **37**: 313–326. https://doi.org/10.1016/j.ympev.2005.07.013

Li H.M., Deng R.Q., Wang X.Z. 2006. Phylogenetic relationships of the Pentatomomorpha (Hemiptera: Heteroptera) inferred from nuclear 18S rDNA sequences. *Zoological Research* **27**: 307–316.

Li M., Tian Y., Zhao Y., Bu W. 2012. Higher level phylogeny and the first divergence time estimation of Heteroptera (Insecta: Hemiptera) based on multiple genes. *PLoS ONE* **7**: e32152. https://doi.org/10.1371/journal.pone.0032152

Lis B., Domagała P.J., Lis J.A. 2023. Tribe Acalyptaini (*Hemiptera: Tingidae*: Tinginae) revisited: can apomorphies in secondary and tertiary structures of 18S rRNA length-variable regions (LVRs) support tribe validity? *Insects* **14**: 600. https://doi.org/10.3390/insects14070600

Lis J.A. 2023. Molecular apomorphies in the secondary and tertiary structures of length-variable regions (LVRs) of 18S rRNA shed light on the systematic position of the family Thaumastellidae (Hemiptera: Heteroptera: Pentatomoidea*). International Journal of Molecula Sciences* **24**: 7758. https://doi.org/10.3390/ijms24097758

Lis J.A, Domagała P.J. 2024. Inconsistencies in the classification of the family Cydnidae (Hemiptera: Heteroptera: Pentatomoidea) revealed by molecular apomorphies in the secondary and tertiary structures of 18S rRNA length-variable region L (LVR L). *International Journal of Molecular Sciences* **25 (2)**: 939. https://doi.org/10.3390/ijms25020939

Lis J.A., Ziaja D., Lis B., Gradowska P.A. 2017. Non-monophyly of the "cydnoid" complex within Pentatomoidea (Hemiptera: Heteroptera) revealed by Bayesian phylogenetic analysis of nuclear rDNA sequences. *Arthropod Systematics & Phylogeny* **75**: 481–496.

McDougall J., Nazar R.N. 1983. Tertiary Structure of the Eukaryotic Ribosomal5 S RNA. *The Journal of Biological Chemistry* **258 (8)**: 5256–5259.

Oren A., Ginzburg M., Ginzburg B.Z., Hochstein L.I., Volcani B.E. 1990. *Haloarcula marismortui* (Volcani) sp. nov., nom. rev., an extremely halophilic bacterium from the Dead Sea. *International Journal of Systematic Bacteriology* **40**: 209–210.

Ouvrard D., Campbell B.C., Bourgoin T., Chan K.L. 2000. 18S rRNA secondary structure and phylogenetic position of Peloridiidae (Insecta, Hemiptera). *Molecular Phylogenetics & Evolution* **16**: 403–417. https://doi.org/10.1006/mpev.2000.0797

Popenda M., Szachniuk M., Antczak M., Purzycka K.J., Lukasiak P., Bartol N., Blazewicz J., Adamiak R.W. 2012. Automated 3D structure composition for large RNAs. Nucleic Acids Research **40(14)**: e112. https://doi.org/10.1093/nar/gks339

Ramakrishnan V. 2011. Molecular biology. The eukaryotic ribosome. *Science (New York, N.Y.)* **331 (6018)**: 681–682. https://doi.org/10.1126/science.1202093

Reuter J.S., Mathews D.H. 2010. RNAstructure: software for RNA secondary structure prediction and analysis. *BMC Bioinformatics* **11**: 129. https://doi.org/10.1186/1471-2105-11-129

Roca-Cusachs M., Schwertner C.F., Kim J., Eger J., Grazia J., Jung S. 2022. Opening Pandora's box: Molecular phylogeny of the stink bugs (Hemiptera: Heteroptera: Pentatomidae) reveals great incongruences in the current classification. *Systematic Entomology* **41**: 36–51. https://doi.org/10.1111/syen.12514

Schrodinger, L.; DeLano,W. PyMOL, Version 2.4.0; Schrodinger, LLC.: New York, NY, USA, 2020. Available online: http://www.pymol.org/pymol

Song N., Li H., Cai W., Yan F., Wang J., Song F. 2016. Phylogenetic relationships of Hemiptera inferred from mitochondrial and nuclear genes. *Mitochondrial DNA* **27**: 4380–4389. https://doi.org/10.3109/19401736.2015.1089538.

Sun F.J., Caetano-Anollés G. 2009. The Evolutionary History of the Structure of 5S Ribosomal RNA. *Journal of Molecular Evolution* **69**: 430–443. https://doi.org/10.1007/s00239-009-9264-z

Sweeney B. A., Hoksza D., Nawrocki E.P., Ribas C.E., Madeira F., Cannone J.J., Gutell R., Maddala A., Meade, C.D., Williams L.D., Petrov A.S., Chan P.P., Lowe T.M., Finn R.D., Petrov A.I. 2021. R2DT is a framework for predicting and visualising RNA seconda-

ry structure using templates. *Nature Communications* **12**: 3494. https://doi.org/10.1038/s41467-021-23555-5

Szymański M., Barciszewska M.Z., Volker A., Erdmann V.A., Barciszewski J. 2003. 5 S rRNA: structure and interactions. *Biochemical Journal* **371**: 641–651.

Szymanski M., Zielezinski A., Barciszewski J., Erdmann V.A., Karlowski W.M. 2016. 5SRNAdb: an information resource for 5S ribosomal RNAs. *Nucleic Acids Research* **44(1)**: 180–183. https://doi.org/10.1093/nar/gkv1081

Taha, H.S.E.-D. 2025. Phylogeny of Trichoplusia ni (Lepidoptera: Noctuidae) 18S and 5S ribosomal RNA gene sequence. *Current Research in Agricultural Sciences* **12(1)**: 35–48.

Taylor D.J., Devkota B., Huang A.D., Topf M., Narayanan E., Sali A., Harvey S.C., Frank J. 2009. Comprehensive molecular structure of the eukaryotic ribosome. *Structure* **17(12)**: 1591–1604. https://doi.org/10.1016/j.str.2009.09.015

The RNAcentral Consortium. 2019. RNAcentral: a hub of information for non-coding RNA sequences. *Nucleic Acids Research* **47**(1): 221–229. https://doi.org/10.1093/nar/gky1034

Vierna J., Wehner S., Zu Siederdissen C.H., Martínez-Lage A., Marz M. 2013. Systematic analysis and evolution of 5S ribosomal DNA in metazoans. *Heredity* **111**: 410–421.

Volarić M., Despot-Slade E., Veseljak D., Pavlek M., Vojvoda Zeljko T., Mravinac B., Meštrović, N. 2024. The genome organization of 5S rRNA genes in the model organism *Tribolium castaneum* and its sibling species *Tribolium freemani*. *Genes* ***15*****(6)**: 776. https://doi.org/10.3390/genes15060776

Wang Y.H., Cui Y., Rédei D., Baňař P., Xie Q., Štys, P., Damgaard, J. Chen P.P., Yi W.B., Wang Y., Dang K., Li Ch.R., Bu W.J. 2016. Phylogenetic divergences of the true bugs (Insecta: Hemiptera:Heteroptera), with emphasis on the aquatic lineages: The last piece of the aquatic insect jigsaw originated in the Late Permian/EarlyTriassic. *Cladistics* **32**: 390–405. https://doi.org/10.1111/cla.12137

Weirauch C., Schuh R.T., Cassis G., Wheeler W.C. 2019. Revisiting habitat and lifestyle transitions in Heteroptera (Insecta: Hemiptera): Insights from a combined morphological and molecular phylogeny. *Cladistics* **35**: 67–105. https://doi.org/10.1111/cla.12233

Wilson D.N., Doudna Cate J.H. 2012. The structure and function of the eukaryotic ribosome. *Cold Spring Harbor perspectives in biology* **4(5)**: a011536. https://doi.org/10.1101/cshperspect.a011536

Wu Y.Z., Yu S.S., Wang Y.H., Wu Y.H., Li X.R., Men X.Y., Zhang Y.W., Rédei D., Xie Q., Bu W.J. 2016. The evolutionary position of Lestoniidae revealed by molecular autapomorphies in the secondary structure of rRNA besides phylogenetic reconstruction (Insecta: Hemiptera: Heteroptera). *Zoological Journal of the Linnean Society* **177**: 750–763. https://doi.org/10.1111/zoj.12385

Wu Y.Z., Rédei D., Eger J. Jr., Wang Y.H., Wu H.Y., Carapezza A., Kment P., Cai B., Sun X.Y., Guo P.L., Luo J.Y., Xie Q. 2018. Phylogeny and the colourful history of jewel bugs (Insecta: Hemiptera: Scutelleridae). *Cladistics* **34**: 502–516. https://doi.org/10.1111/cla.12224

Xie Q., Bu W., Zheng L. 2005. The Bayesian phylogenetic analysis of the 18S rRNA sequences from the main lineages of Trichophora (Insecta: Heteroptera: Pentatomomorpha). *Molecular Phylogenetics & Evolution* **34**: 448–451. https://doi.org/10.1016/j.ympev.2004.10.015

Xie Q., Tian Y., Zheng L., Bu W. 2008. 18S rRNA hyperelongation and the phylogeny of Euhemiptera (Insecta: Hemiptera). *Molecular Phylogenetics & Evolution* **47**: 463–471. https://doi.org/10.1016/j.ympev.2008.01.024

Yu S., Wang Y., Rédei D., Xie Q., Bu W. 2013. Secondary structure models of 18S and 28S rRNAs of the true bugs based on complete rDNA sequences of *Eurydema maracandica* Oshanin, 1871 (Heteroptera, Pentatomidae). *ZooKeys* **319**: 363–377. https://doi.org/10.3897/zookeys.319.4178

This work is licensed under a Creative Commons Attribution 4.0 International License http://creativecommons.org/licenses/by/4.0/

Received: 10 November 2025
Accepted: 5 December 2025