EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz

Eur. J. Entomol. **121**: 413–424, 2024
doi: 10.14411/eje.2024.045

REVIEW

The number of testicular follicles and ovarioles in Cicadomorpha (Hemiptera: Auchenorrhyncha): Variability and evolutionary trends

Valentina G. KUZNETSOVA and **Natalia V. GOLUB**

Department of Karyosystematics, Zoological Institute, Russian Academy of Sciences, Universitetskaya emb. 1, St. Petersburg 199034, Russia; e-mails: valentina.kuznetsova@zin.ru, nvgolub@mail.ru

Key words. Testes, ovaries, diversity, Cicadoidea, Cercopoidea, Membracoidea

Abstract. The hemipteran infraorder Cicadomorpha (cicadas, leafhoppers, treehoppers and spittlebugs) comprises more than 30,000 described extant species in 3,783 genera, 13 families and 3 superfamilies: Cicadoidea, Cercopoidea and Membracoidea. Here, we summarize and discuss data on the number of testicular follicles in 103 species belonging to 84 genera and 9 families of Cicadoidea (Tettigarctidae and Cicadidae), Cercopoidea (Aphrophoridae, Cercopidae and Ischnorhinidae) and Membracoidea (Aetalionidae, Cicadellidae, Membracidae and Myerslopiidae), as well as the number of ovarioles in 65 species belonging to 56 genera of the same families, except for Tettigarctidae, Aetalionidae, and Myerslopiidae, for which no such data were available. Almost 83% of the species and 81% of the genera studied belong to the family Cidadellidae. In general, the number of follicles in Cicadomorpha ranges from 1 to "about 100 or more" per testis, and the number of ovarioles from 3 to over 70–80 per ovary. The highest numbers are characteristic of Cicadoidea and Cercopoidea, with significantly higher values in the former superfamily. In Membracoidea, both follicle and ovariole numbers vary within markedly narrower limits. Most taxa are dominated by testes each consisting of 6 follicles, and the ovaries each consisting of 6 ovarioles. These character states are considered ancestral for Cicadomorpha, and possibly for Auchenorrhyncha as a whole.

INTRODUCTION

The hemipteran infraorder (sometimes referred to as suborder, e.g. Chen et al., 2019a) Cicadomorpha Evans, 1946 (cicadas, leafhoppers, treehoppers and spittlebugs), is the largest group of Hemiptera and a sister lineage to the infraorder Fulgoromorpha (planthoppers) within Auchenorrhycha (Cryan & Urban, 2012; Skinner et al., 2020). Cicadomorpha includes approximately 30,000 to 35,000 described extant species of plant sap-sucking insects distributed worldwide, excluding the Arctic and Antarctic (Dietrich, 2005; Song et al., 2017; Bartlett et al., 2018; Szwedo, 2018). In general, the infraorder is subdivided into three superfamilies, Cicadoidea, Cercopoidea and Membracoidea (Dietrich, 2002; Crayan, 2005; Dietrich et al., 2017; Song et al., 2017; Bartlett et al., 2018), or into 5 superfamilies with the addition of Cicadelloidea and Myerslopioidea to the above three (Szwedo, 2018).

The history of the study of the internal reproductive organs of Cicadomorpha began with the work of Dufour (1833), who described and illustrated the various parts of the male and female reproductive systems of several species, including testes and ovaries in terms of the number of follicles and ovarioles, respectively. This was followed by publications on the structure of the testes and ovaries in individual members of the infraorder (e.g., Holmgren, 1899; Gadd, 1910; Ivanov, 1926; Helms, 1968; Mishra, 1979; Kaplin, 1985; Bednarczyk, 1983, 1993; Kuznetsova & Kirilova, 1993; Cheung, 1994; Tsai & Perrier, 1996; Lupa et al., 1999), including fairly recent publications (e.g., Hayashi & Kamimura, 2002; Hummel et al., 2006; Golub et al., 2014; Vitale et al., 2015; Pappalardo et al., 2016; Araújo et al., 2020; Silva, 2022; Chen et al., 2023; Özyurt Koçakoğlu et al., 2024a, b; Sodré et al., 2024).

In general, the internal reproductive system of Cicadomorpha does not differ from that of Fulgoromorpha, for which similar data were recently published (Kuznetsova et al., 2024). Males have paired testes with varying numbers of seminal follicles, two efferent ducts united in a median common duct, seminal vesicles, accessory glands and a median ejaculatory duct. Females have paired ovaries with varying numbers of ovarioles, a pair of lateral oviducts, a spermatheca, a copulatory bursa and a vagina.

Kuznetsova et al. (2024) summarised all available data on the number of testicular follicles and ovarioles in representatives of 17 planthopper families (186 species, 123 genera, from both superfamilies, Delphacoidea and Fulgoroidea). It was shown that the number of follicles is a species-specific trait, typically stable within species and, in some cases, invariant at higher taxonomic levels. The number of follicles varies from 3 to 30 per testis; the most common numbers are 6, 4 and 3 (with 10 in the family Issidae). The presumed ancestral number is 6, which can vary either upwards or downwards in individual families, probably due to polymerisation or oligomerisation. In contrast, the number of ovarioles can vary even within species, presumably depending on biological or environmental factors, making it harder to detect evolutionary trends. However, in some families, such as the well-studied family Dictyopharidae, such trends are quite apparent (Kuznetsova et al., 2024).

The aim of the present study was to establish the diversity of follicle and ovariole numbers in Cicadomorpha and to identify the main trends in their variability both within individual families and across the infraorder as a whole.

MATERIAL AND METHODS

The present paper is part of a series of our original and review papers on the structure of the internal reproductive system in various insect orders, such as Mantophasmatodea (Lachowska-Cierlik et al., 2015), Zoraptera (Kuznetsova et al., 2002), Psocoptera, Mallophaga and Anoplura (Emeljanov et al., 2001), Neuroptera (Kuznetsova et al., 2019), and Hemiptera (Maryańska-Nadachowska et al., 2001a, b; Kuznetsova et al., 2012; Grozeva et al., 2022), including the infraorder Fulgoromorpha (Kuznetsova et al., 2024). Unlike the latter, which largely comprised the authors' own data, this review is based almost exclusively on an analysis of the literature. All species studied, with their respective number of follicles and ovarioles, are listed in Table 1. Species are categorised by genera, tribes and subfamilies within their respective families. The classification of Cicadomorpha and the number of species and genera within each family are in accordance with Bartlett et al. (2018) and/or Dmitriev et al. (2022). The Conclusions section provides a brief assessment of the diversity of the analyzed characters and identifies the main evolutionary trends, both in Cicadomorpha and in Auchenorrhyncha as a whole.

RESULTS AND DISCUSSION

Cicadomorpha (cicadas, leafhoppers, treehoppers and spittlebugs) is the largest infraorder of Hemiptera, with over 30,000 described species in 3,783 genera, 13 families and 3 superfamilies: Cicadoidea Latreille, 1802; Cercopoidea Leach, 1815; and Membracoidea Rafinesque, 1815 (Bartlett et al., 2018). Follicle number data are currently available for 9 families (103 species, 84 genera, all 3 superfamilies). Data on the numbers of ovarioles are known for 6 families (65 species, 57 genera, all 3 superfamilies). Such data are unavailable for the families Clastopteridae Dohrn, 1859 and Machaerotidae Stål, 1866 (Cercopoidea) with 85 and 118 species, respectively, as well as for two smaller families: Epipygidae Hamilton, 2001 (Cercopoidea) with only 4 species, and Melizoderidae Deitz & Dietrich, 1993 (Membracoidea) with just 8 species. Comments on each family studied are given below.

Superfamily Cicadoidea Latreille, 1802

Cicadoidea (cicadas) comprises 2,895 species worldwide in 428 genera and two extant families, Cicadidae Latreille, 1802 and Tettigarctidae (Bartlett et al., 2018). Data are available for both of them.

Tettigarctidae Distant, 1905 (hairy cicadas) is a relict family, containing only two extant species in the genus *Tettigarcta* White, 1845 (Bartlett et al., 2018). According to Moulds (2005), both of these species have "many (perhaps 100 or more)" follicles per testis. Data on ovarioles are not available.

Cicadidae Latreille, 1802 (true cicadas) is a large family with 2,893 species in 427 genera, 55 tribes and 3 subfamilies: Cicadinae, Cicadettinae and Tibicininae (Bartlett et al., 2018; Dmitriev et al., 2022). They occur worldwide, though they are more common in the tropical region. Data on follicles and/or ovarioles are available for the subfamilies Cicadinae (includes 1,611 species, 191 genera, 30 tribes) and Cicadettinae (includes 1,103 species, 212 genera, 12 tribes). Males of 27 species (20 genera, 12 tribes) were studied, 15 species (10 genera, 9 tribes) from the first subfamily and 12 (10 genera, 3 tribes) from the second. As in Tettigarctidae, the testes of Cicadidae species have a large number of follicles. Different authors estimate their number in each testis of the studied species as either "at least a hundred" (Dufour, 1833) or "numerous (perhaps 100 or more)" (Moulds, 2005). Tian et al. (2006), who studied *Hyalessa maculaticollis*, do not mention the number of follicles but provide a schematic representation of a testis with a large number of follicles. Of interest are the data on ovaries available for only three species of Cicadinae. While the ovary of *Arunta perulata* (Thophini) has "perhaps 100 or more" ovarioles (Moulds, 2005: Fig. 29) and the ovary of *Cicada orni* (Cicadini) has "about 70–80 ovarioles" (Dufour, 1833), the third species, *Cicadatra atra* (Cicadatrini), has 6 ovarioles in each ovary (Gadd, 1910). Thus, the number of follicles and ovarioles in Cicadidae is very high, the highest found so far in Auchenorrhyncha as a whole. Moulds (2005) considers numerous follicles to be a diagnostic feature of the entire superfamily Cicadoidea. Based on the available data, it can be assumed that in the ancestor of this group, the testes and ovaries already consisted of a large number of follicles and ovarioles. Nevertheless, data remain quite scarce, and the finding of 6 ovarioles in *C. atra* (a number considered to be primitive in the evolution of ovarioles and testicular follicles in Auchenorrhyncha; Emeljanov & Kuznetsova, 1983) allows us to propose an alternative hypothesis about the initial structure of the gonads in Cicadidae (see Conclusions).

Superfamily Cercopoidea Leach, 1815

Cercopoidea (spittlebugs or froghoppers) comprises over 2,600 species worldwide in 366 genera and 5 families (Bartlett et al., 2018). Data are available for the families Aphrophoridae and Cercopidae, which are considered sister taxa (Chen et al., 2019b), as well as for the family Ischnorhinidae.

Aphrophoridae Amyot & Audinet-Serville, 1843 is a medium-sized family with 925 species, 157 genera and 8 tribes, within the only recognized subfamily Aphrophorinae (Bartlett et al., 2018; Dmitriev et al., 2022). Data on follicles and/or ovarioles are available for 12 species, 7 genera, and 3 tribes: Philaenini, Aphrophorini and Clovini.

Table 1. Number of follicles and ovarioles in 9 families of Cicadomorpha.

Taxa	Locality	Number of		References
		follicles per testis	ovarioles per ovary	
CICADOIDEA				
1. TETTIGARCTIDAE				
Tettigarctinae				
Tettigarctini				
1. *Tettigarcta crinita* Distant, 1883	Australia	"numerous*"	–	Moulds, 2005
2. *T. tomentosa* White, 1845	Australia	"numerous*"	–	Moulds, 2005
2. CICADIDAE				
Cicadinae				
Arenopsaltriini				
3. *Henicopsaltria eydouxii* (Guérin-Méneville, 1838)	Australia	"numerous*"	–	Moulds, 2005
4. *H. rufivelum* Moulds, 1978	Australia	"numerous*"	–	Moulds, 2005
Burbungini				
5. *Burbunga albofasciata* Distant, 1907	Australia	"numerous*"	–	Moulds, 2005
6. *B. gilmorei* (Distant, 1882)	Australia	"numerous*"	–	Moulds, 2005
7. *B. hillieri* (Distant, 1907)	Australia	"numerous*"	–	Moulds, 2005
Cicadatrini				
8. *Cicadatra atra* (Olivier, 1790)	Ukraine	–	6	Gadd, 1910
Cicadini				
9. *Cicada orni* Linnaeus, 1758	France	"at least a hundred"	"about 70–80"	Dufour, 1833
Cyclochilini				
10. *Cyclochila australasiae* (Donovan, 1805)	Australia	"numerous*"	–	Moulds, 2005
11. *C. virens* Distant, 1906	Australia	"numerous*"	–	Moulds, 2005
Macrotristriini				
12. *Macrotristria angularis* (Germar, 1834)	Australia	"numerous*"	–	Moulds, 2005
13. *M. intersecta* (Walker, 1850)	Australia	"numerous*"	–	Moulds, 2005
Psaltodini				
14. *Psaltoda moerens* (Germar, 1834)	Australia	"numerous*"	–	Moulds, 2005
Sonatini				
15. *Hyalessa maculaticollis* (Motschulsky, 1866)	China	numerous	–	Tian et al., 2006: Fig. 1a (as *Oncotympana*)
Tamasini				
16. *Parnkalla muelleri* (Distant, 1882)	Australia	"numerous*"	–	Moulds, 2005
17. *Tamasa tristigma* (Germar, 1834)	Australia	"numerous*"	–	Moulds, 2005
Thophini				
18. *Arunta perulata* (Guérin-Méneville, 1831)	Australia	"numerous*"	numerous	Moulds, 2005: Fig 29
Cicadettinae				
Cicadettini				
19. *Atrapsalta encaustica* (Germar, 1834)	Australia	"numerous*"	–	Moulds, 2005 (as *Pauropsalta*)
20. *Birrima castanea* (Goding & Froggatt, 1904)	Australia	"numerous*"	–	Moulds, 2005
21. *Diemeniana frenchi* (Distant, 1907)	Australia	"numerous*"	–	Moulds, 2005
22. *Palapsalta circumdata* (Walker, 1852)	Australia	"numerous*"	–	Moulds, 2005 (as *Pauropsalta*)
23. *P. eyrei* (Distant, 1882)	Australia	"numerous*"	–	Moulds, 2005 (as *Pauropsalta*)
24. *Pauropsalta mneme* (Walker, 1850)	Australia	"numerous*"	–	Moulds, 2005
25. *Pauropsalta* sp.	Australia	"numerous*"	–	Moulds, 2005
Chlorocystini				
26. *Chlorocysta vitripennis* (Westwood, 1851)	Australia	"numerous*"	–	Moulds, 2005
27. *Cystosoma saundersii* (Westwood, 1842)	Australia	"numerous*"	–	Moulds, 2005
28. *Guineapsaltria flava* (Goding & Froggatt, 1904)	Australia	"numerous*"	–	Moulds, 2005
Lamotialnini				
29. *Aleeta curvicosta* (Germar, 1834)	Australia	"numerous*"	–	Moulds, 2005
30. *Magicicada septendecim* (Linnaeus, 1758)	Australia	"numerous*"	–	Moulds, 2005
CERCOPOIDEA				
3. APHROPHORIDAE				
Aphrophorinae				
Aphrophorini				
31. *Aphrophora alni* (Fallén, 1805)	Ukraine Sweden	28–35 –	11–13 6	Ivanov, 1926 Holmgren, 1899
32. *A. memorabilis* Walker, 1858	China	"many"	–	Tian et al., 2006
33. *A. intermedia* Uhler, 1896	China	"many"	–	Tian et al., 2006
34. *A. salicina* (Goeze, 1778)	France	"about 20"	"about 15"	Dufour, 1833
35. *Aphropsis gigantea* Metcalf & Horton, 1934	China	"many"	–	Tian et al., 2006
36. *Philagra albinotata* Uhler, 1896	China	"many"	–	Tian et al., 2006
Clovini				
37. *Clovia punctum* (Walker, 1851)	India Egypt China	17 17 "many"	– – –	Mishra, 1979 Ammar, 1985 Tian et al., 2006
38. *Lepyronia coleoptrata* (Linnaeus, 1758)	Ukraine China	21-28 "many"	19–20 –	Ivanov, 1926; Tian et al., 2006 (about 18 based on Fig. 1d)
Philaenini				
39. *Neophilaenus campestris* (*Fallén*, 1805)	Sweden	–	6	Holmgren, 1899 (as *Philaenus*)
40. *N. lineatus* (Linnaeus, 1758)	Sweden	–	10	Holmgren, 1899 (as *Philaenus*)
41. *Philaenus arslani* Abdul-Nour & Lahoud, 1996	Lebanon	10–11–12	–	Maryańska-Nadachowska et al., 2008
42. *Ph. spumarius* (Linnaeus, 1758)	Ukraine Sweden China	12 – "many"	12 9 –	Ivanov, 1926 Holmgren, 1899 Tian et al., 2006
4. CERCOPIDAE				
Cercopinae				
Cercopini				
43. *Cercopis vulnerata* (Rossi, 1807)	Turkey	1	14	Özyurt Koçakoğlu et al., 2024 a, b
44. *C. sanguinolenta* (Scopoli, 1763)	France	–	"about 30"	Dufour, 1833

	Callitettigini				
45.	*Callitettix versicolor* (Fabricius, 1794)	China	“many”	–	Tian et al., 2006
	Cosmoscartinae				
	Cosmoscartini				
46.	*Cosmoscarta abdominalis* (Donovan, 1798)	China	“many”	–	Tian et al., 2006 [as *C. heros* (Fabricius)]
47.	*C. bispecularis* (White, 1844)	China	“many”	–	Tian et al., 2006 [as *C. bimacula* (Walker)]
48.	*Phymatostetha dorsivitta* Walker, 1851	China	“many”	–	Tian et al., 2006
	5. ISCHNORHINIDAE				
	Ischnorhininae				
	Tomaspidini				
49.	*Mahanarva fimbriolata* (Stål, 1854)	Brazil	36–38	–	Sodré et al., 2024
	MEMBRACOIDEA				
	6. AETALIONIDAE				
	Aetalioninae				
	Aetalionini				
50.	*Aetalion reticulatum* (Linnaeus, 1767)	Costa Rica	9	–	Kuznetsova & Kirilova, 1993
		Brasil	4	–	Araújo et al., 2020 (as *Aethalium reticulatum*)
	7. CICADELLIDAE				
	Aphrodinae				
	Aphrodini				
51.	*Anoscopus flavostriatus* (Donovan, 1799)	Poland	6	–	Bednarczyk, 1993
52.	*Aphrodes bicincta* (Schrank, 1776)	Ukraine	7	7	Ivanov, 1926 (as *Acocephalus nervosus* Schr.)
		Poland	7	–	Bednarczyk, 1993
53.	*Stroggylocephalus agrestis* (Fallén, 1806)	Poland	14	–	Bednarczyk, 1993
	Cicadellinae				
	Cicadellini				
54.	*Bothrogonia ferruginea* (Fabricius, 1787)	Japan	11–13	–	Hayashi & Kamimura, 2002
55.	*Cicadella viridis* (Linnaeus, 1758)	Ukraine	–	6	Gadd, 1910 (as *Tettigonia*)
		Ukraine	6	6	Ivanov, 1926 (as *Tettigonia*)
		China	6	–	Zhang et al., 2016
		China	6?	–	Tian et al., 2006: Fig.1c
56.	*Cofana spectra* (Distant, 1908)	?	3	–	Mishra, 1979
		Poland	3	–	Bednarczyk, 1993 (as *Cicadella*)
57.	*C. unimaculata* (Signoret, 1854)	?	5	–	Mishra, 1979 (as *Kolla*)
		Poland	5	–	Bednarczyk 1993 (as *Kolla*)
58.	*Kolla paulula* (Walker, 1858)	China	5	–	Zhang et al., 2016
	Proconiini				
59.	*Homalodisca vitripennis* (Germar, 1821)	USA, CA	–	10	Hummel et al., 2006 [as *H. coagulata* (Say)]
	Deltocephalinae				
	Athysanini				
60.	*Allygus mixtus* (Fabricius, 1794)	Sweden	–	6	Holmgren, 1899 (as *Thamnotettix*)
61.	*Artianus interstitialis* (Germar, 1821)	Ukraine	12	12	Ivanov, 1926 (as *Athysanus*)
		Poland	12	–	Bednarczyk, 1993 (as *Athysanus*)
62.	*Euscelis incisa* (Kirschbaum, 1858)	Poland	7	–	Bednarczyk, 1993 (as *E. plebeius* Fall.)
		Sweden	–	6	Holmgren, 1899 (as *Thamnotettix plebeja* Fall.)
63.	*Euscelidius variegatus* (Kirschbaum, 1858)	USA	–	7	Cheung, 1994 (as *Euscelidium*)
64.	*Handianus ulugbegi* Dlabola, 1960	Turkmenistan	–	7	Kaplin, 1985
65.	*Hesium domino* (Reuter, 1880)	Ukraine	–	12	Ivanov, 1926 (as *Thamnotettix biguttatus* Fall.)
66.	*Laburrus impictifrons* (Boheman, 1852)	Ukraine	12	8	Ivanov, 1926 (as *Bithoscopus flavicollis* L.)
		Poland	8–9	–	Bednarczyk, 1993 (as *Athysanus*)
	Cicadulini				
67.	*Cicadula quadripunctata* (De Villers, 1789)	Ukraine	8	8	Ivanov, 1926 (as *Thamnotettix quadrinotatus* F.)
		Poland	8	–	Bednarczyk, 1993 (as *C. quadrinotata* F.)
68.	*Mocydia crocea* (Herrich-Schäffer, 1837)	Poland	6	7	Bednarczyk, 1993
	Chiasmini				
69.	*Doratura homophyla* (Flor, 1861)	Poland	6	–	Bednarczyk, 1993
70.	*D. stylata* (Boheman, 1847)	Poland	6	–	Bednarczyk, 1993
71.	*Exitianus indicus* (Distant, 1908)	?	6	–	Chen et al., 2023 with ref. to Su et al., 2014**
72.	*Nephotettix cincticeps* Uhler, 1896	China	6	6	Chen et al., 2023
	Deltocephalini				
73.	*Deltocephalus pulicaris* (Fallén, 1806)	Poland	6	–	Bednarczyk, 1993
74.	*D. vulgaris* Dash & Viraktamath, 1998	China	5	6	Chen et al., 2023
75.	*Graminella nigrifrons* (Forbes, 1885)	North America	6	6	Tsai & Perrier, 1996
	Eupelicini				
76.	*Paradorydium* sp.	Turkmenistan	–	6	Kaplin, 1985
	Macrostelini				
77.	*Balclutha brevis* Lindberg 1954	Italy, Sicily	6	–	Vitale et al., 2015
			–	6	Pappalardo et al., 2016
78.	*Dalbulus maidis* (DeLong, 1923)	North America	6	6	Tsai & Perrier, 1996
79.	*Macrosteles cristatus* (Ribaut, 1927)	Poland	5	–	Bednarczyk, 1993
80.	*M. sexnotatus* (Fallén, 1806)	Ukraine	–	6	Ivanov, 1926 (as *Cicadula*)
		Berkshire, UK	6	6	Becker, 1979
		Egypt	–	6	Ammar, 1985
81.	*Sagatus punctifrons* (Fallén, 1826)	Poland	6	–	Bednarczyk, 1993
	Opsiini				
82.	*Diacra pinguis* Emeljanov, 1969	Turkmenistan	–	8	Kaplin, 1985
	Paralimnini				
83.	*Diplocolenus abdominalis* (Fabricius, 1803)	Sweden	–	6	Holmgren, 1899
84.	*Prosperellus ephemericus* (Emeljanov, 1979)	Turkmenistan	–	6	Kaplin, 1985 (as *Cabrellus*)
85.	*Psammotettix alienus* (Dahlbom, 1850)	Turkmenistan	–	6	Kaplin, 1985 [as *Psammotettix striatus* (L.)]
		?	6	–	Chen et al., 2023 with ref. to Su et al., 2014**
	Platymetopiini				
86.	*Platymetopius chloroticus* Puton, 1877	Turkmenistan	–	6	Kaplin, 1985
	Stenometopiini				
87.	*Anaconura aristidae* (Emeljanov, 1968)	Turkmenistan	–	6	Kaplin, 1985 (as *Stirellus*)

Eurymelinae				
Idiocerini				
88. *Amritodus atkinsoni* (Lethierry, 1889)	India Poland	6 6	– –	Mishra, 1979 Bednarczyk, 1993
89. *Idiocerus lituratus* (Fallén, 1806)	Ukraine	6	16–18	Ivanov, 1926
90. *Metidiocerus rutilans* (Kirschbaum, 1868)	Poland	6	–	Bednarczyk, 1993 (as *Idiocerus*)
91. *Populicerus populi* (Linnaeus, 1761)	Poland	6	–	Bednarczyk, 1983
92. *Rhytidodus nobilis* (Fieber, 1868)	Ukraine	–	20–23	Ivanov, 1926 (as *Idiocerus*)
Macropsini				
93. *Macropsis impura* (Boheman, 1847)	Poland	6	–	Bednarczyk, 1993
94. *Oncopsis flavicollis* (Linnaeus, 1761)	Ukraine Poland	6 3	8 –	Ivanov, 1926 (as *Athysanus impictifrons* Boh.) Bednarczyk, 1993
Evacanthinae				
Evacanthini				
95. *Evacanthus interruptus* (Linnaeus, 1758)	Sweden Poland	– 6	6 –	Holmgren, 1899 Bednarczyk, 1993
Ledrinae				
Ledrini				
96. *Ledra aurita* (Linnaeus, 1758)	France	–	10–12	Dufour, 1833
97. *Neotituria kongosana* (Matsumura, 1915)	South Korea	–	7	Lupa et al., 1999
Megophthalminae				
Adelungiini				
98. *Achrus albicosta* (Kusnezov, 1929)	Turkmenistan	–	11	Kaplin, 1985
99. *A. flavovirens* Lindberg, 1925	Turkmenistan	–	12	Kaplin 1985
100. *A. prodigiosus* (Melichar, 1902)	Turkmenistan	–	9–11	Kaplin, 1985 (as *Achrus robustus* Ldb., 1929)
101. *Bergevina ahngeri* (Melichar, 1902)	Turkmenistan	–	15–16	Kaplin, 1985 (as *Achrus*)
102. *Melicharella paradisea* Emeljanov, 1975	Turkmenistan	–	12	Kaplin, 1985
103. *M. planifrons* (Melichar, 1902)	Turkmenistan	–	12, 12–13	Kaplin, 1985
104. *Pleopardus rubiginosus* (Mitjaev, 1969)	Turkmenistan	–	13	Kaplin, 1985
105. *Spathicerula calligoni* (Oshanin, 1908)	Turkmenistan	–	10	Kaplin, 1985 (as *Adelungia*)
106. *Symphypyga obsoleta* Haupt, 1917	Turkmenistan	–	16	Kaplin, 1985
107. *S. repetekia* Kusnezov, 1929	Turkmenistan	–	15	Kaplin, 1985
Agalliini				
108. *Agallia brachyptera* (Boheman, 1847)	Poland	6	–	Bednarczyk, 1993
109. *A. constricta* Van Duzee, 1894	Poland USA Egypt	6 6 –	– 6 6	Bednarczyk, 1993 Gil-Fernandez & Black, 1965 Ammar, 1985
110. *Agalliota quadripunctata* (Provancher, 1872)	Egypt	–	6	Ammar, 1985
111. *Anaceratagallia ribauti* (Ossiannilsson, 1938)	Poland	6	–	Bednarczyk, 1993
112. *A. venosa* (Fourcroy, 1785)	Ukraine	–	6	Ivanov, 1926 (as *Agallia*)
Typhlocybinae				
Alebrini				
113. *Alebra albostriella* (Fallén, 1826)	Poland	5	–	Bednarczyk, 1993
Dikraneurini				
114. *Forcipata citrinella* (Zetterstedt, 1828)	Poland	3	–	Bednarczyk, 1993
115. *Notus flavipennis* (Zetterstedt, 1828)	Poland	3	–	Bednarczyk, 1993
Empoascini				
116. *Empoasca fabae* (Harris, 1841)	USA, Iowa Poland	4 4	4 –	Helms, 1968; Bednarczyk, 1993
117. *Hebata vitis* (Göthe, 1875)	Poland	4		Bednarczyk, 1993 (as *Empoasca*)
118. *Kyboasca bipunctata* (Oshanin, 1871)	Ukraine	–	4	Ivanov, 1926 (as *Chlorita*)
119. *Kybos smaragdula* (Fallén, 1806)	Sweden Poland	– 4	3 –	Holmgren, 1899 (as *Cicadula*) Bednarczyk, 1993
Erythroneurini				
120. *Alnetoidia alneti* (Dahlbom, 1850)	Poland	3	–	Bednarczyk, 1983 (as *Alnetoidea*)
121. *Arboridia parvula* (Boheman, 1845)	Ukraine	–	3	Ivanov, 1926 (as *Zygina*)
122. *Zygina flammigera* (de Fourcroy, 1785)	Ukraine Poland	4 4	–	Ivanov, 1926 Bednarczyk, 1993
123. *Zyginidia viaduensis* (Wagner, 1941)	Poland	2	–	Bednarczyk, 1993
Typhlocybini				
124. *Edwardsiana flavescens* (Fabricius, 1794)	Ukraine	4	4	Ivanov, 1926 (as *Chlorita*)
125. *E. lethierryi* (Edwards, 1881)	Poland	3	–	Bednarczyk, 1993 [as *Edwardsiana hippocastani* (Edw.)]
126. *Eupteryx atropunctata* (Goetze, 1778)	Ukraine	–	3	Ivanov, 1926
127. *E. urticae* (Fabricius, 1803)	Ukraine	3	6	Ivanov, 1926
128. *E. vittata* (Linnaeus, 1758)	Sweden	–	3	Holmgren, 1899
129. *Fagocyba cruenta* (Herrich-Schäffer, 1838)	Poland	3	–	Bednarczyk, 1993
130. *Ribautiana ulmi* (Linnaeus, 1758)	Poland	3	–	Bednarczyk, 1993
Ulopinae				
Ulopini				
131. *Utecha trivia* Germar, 1821	Ukraine Poland	4 4	– –	Ivanov, 1926 (as *Ulopa*) Bednarczyk, 1993
8. MEMBRACIDAE				
Membracinae				
Aconophorini				
132. *Calloconophora argentipennis* Dietrich, 1991	Brasil	14	–	Silva, 2022
Membracini				
133. *Campylenchia latipes* (Say, 1824)	Brasil	8	–	Silva, 2022
Centrotinae				
Centrotini				
134. *Centrotus cornutus* (Linnaeus, 1758)	Ukraine	–	10–12	Ivanov, 1926
Gargarini				
135. *Gargara genistae* (Fabricius, 1775)	Ukraine China	6–8 6	6–8 –	Ivanov, 1926 Tian et al., 2006 (based on Fig. 1b)
Leptocentrini				
136. *Otinotus elongatus* Distant, 1908	Egypt	4		Ammar, 1985
Nicomiinae				
137. *Tolania opponens* Walker, 1858	Mexico	8	–	Kuznetsova & Kirillova, 1993
9. MYERSLOPIIDAE				
Myerslopiinae				
138. *Mapuchea chilensis* (Nielson, 1996)	Chile	6/6, 6/5***, 6/4***	–	Golub et al., 2014

* "Numerous (perhaps 100 or more)" (Moulds, 2005). ** No information on the number of follicles in Su et al. (2014). *** Different numbers of follicles/ovarioles in different testes/ovaries of the same specimen.

Both testes and ovaries consist of a relatively large number of follicles and ovarioles, respectively, and in many cases, the number per species was not determined with precision. The number of follicles (in a testis) in the 10 studied species ranges from 12 in *Philaenus spumarius* (Philaenini) to 28–35 in *Aphrophora alni* (Aphrophorini), with a few intermediate values. In some cases, the number of follicles in a species is estimated as "many" (Tian et al., 2006), such as in *Philaenus spumarius* and *Lepyronia coleoptrata*. Since other authors have cited numbers of 12 and 21–28 for these species, respectively, "many" probably refers to a number not exceeding the upper limit of 28–35 for the family. The number of ovarioles in the six studied species varies from 6 in *A. alni* from Sweden (it should be noted that the same species from Ukraine has 11–13 ovarioles per ovary) and *Neophilaenus campestris* (Philaenini) to 19–20 per ovary in *Lepyronia coleoptrata* (Clovini). Intermediate numbers are 9 in *Philaenus spumarius* from Sweden (although the same species from Ukraine has 12 ovarioles per ovary), 10 in *Neophilaenus lineatus* (Philaenini) and "about 15" in *Aphrophora salicina* (Aphrophorini).

Cercopidae Westwood, 1838, with 1,480 species, 173 genera and 11 tribes in two subfamilies, Cercopinae and Cosmoscartinae, is the most species-rich spittlebug family (Bartlett et al., 2018). Data on follicles and/or ovarioles are available for six species from 4 genera and 3 tribes across both subfamilies. *Cercopis vulnerata* (Cercopinae: Cercopini) is the only species of Auchenorrhyncha described as having a single follicle per testis (Özyurt Koçakoğlu et al., 2024a). Another studied species from this subfamily, *Callitettix versicolor* (Callitettigini), and all three studied species of the subfamily Cosmoscartinae (tribe Cosmoscartini) have "many follicles" in the testis (Tian et al., 2006). Data on ovarioles are available only for Cercopinae, in which *Cercopis vulnerata* and *C. sanguinolenta* have 14 and "about 30" ovarioles per ovary, respectively.

Ischnorhinidae Schmidt, 1920 is a New World family with 450 valid species in 60 genera and three tribes: Tomaspidini, Ischnorhinini and Neaenini, all in the subfamily Ischnorhininae (Dmitriev et al., 2022). The only species studied, *Mahanarva fimbriolata* (Tomaspidini), has "36–38 (36 on average)" follicles per testis (Sodré et al., 2024).

Superfamily Membracoidea Rafinesque, 1815

Membracoidea (treehoppers and leafhoppers) is the largest superfamily of Cicadomorpha, with approximately 25,000 species worldwide in 2,489 genera and five families, including three treehopper families, Aetalionidae, Melizoderidae and Membracidae, and two leafhopper families, Cicadellidae (true leafhoppers) and Myerslopiidae (ground-dwelling leafhoppers) (Bartlett et al., 2018). Data are available for 89 species, 76 genera and all families except the small South American family Melizoderidae, which has only 10 species in three genera (Dmitriev et al., 2022).

Aetalionidae Spinola, 1850 is a small family, with 42 species, 6 genera and two tribes in two subfamilies, Aetalioninae and Biturritiinae (Dmitriev et al., 2022). The family is predominantly Neotropical, but the only studied genus, *Aetalion* Latreille, 1810 (Aetalioninae), has been recorded from both Neotropical and Nearctic regions (Dietrich, 2005). Males of *Aetalion reticulatum* collected from an unidentified host plant in Costa Rica (Central America) have 9 follicles in the testis (Kuznetsova & Kirillova, 1993), while males collected from *Trema micrantha* (Linnaeus, 1767) in Brazil have 4 follicles per testis (Araújo et al., 2020). Manual anatomization was used in the first case and histological techniques in the second. In follicle counting, the first method seems to be more reliable, but such a significant discrepancy in the data may be due to other reasons.

Cicadellidae Latreille, 1802, with more than 23,000 described species worldwide (excluding Antarctica) in approximately 2,550 genera and 128 tribes grouped into 19 subfamilies, is the largest family not only of Auchenorrhyncha (> 43,000 known species) but also of hemimetabolous insects in general (Bartlett et al., 2018; Dietrich et al., 2022; Dmitriev et al., 2022; Hu et al., 2022; Evangelista et al., 2024). Data on follicles and/or ovarioles are available for 81 species, 68 genera and 26 tribes in 9 subfamilies, including Aphrodinae, Cicadellinae, Deltocephalinae, Eurymelinae, Evacanthinae, Ledrinae, Megophthalminae, Typhlocybinae, and Ulopinae.

Aphrodinae. There are 270 species in 14 genera and 4 tribes (Bartlett et al., 2018; Dmitriev et al., 2022). Data on follicles and/or ovarioles are available for three species from three genera of the tribe Aphrodini. Each of the species studied has a different number of follicles: 6, 7, and 14 per testis, respectively. Note that the species with 7 follicles per testis, *Aphrodes bicincta*, has the same number of ovarioles per ovary.

Cicadellinae. There are about 2,600 species in 340 genera and 5 tribes (Dmitriev et al., 2022). Data are available for 6 species, 5 genera, and 2 tribes. Five species (4 genera) of the tribe Cicadellini have four values of follicle number: 3, 5, 6 and 11–13. Among these species, *Cicadella viridis* has the same number of follicles and ovarioles, namely 6 in both cases. There are no other data on ovarioles for this tribe. The only studied species of the tribe Proconiini, *Homalodisca vitripennis*, has 10 ovarioles per ovary.

Deltocephalinae. There are more than 7,000 species in 930 genera and 40 tribes (Bartlett et al., 2018; Dmitriev et al., 2022). A large amount of data has been accumulated for this subfamily. In total, data on follicles and/or ovarioles are available for 28 species from 25 genera and 10 tribes: Athysanini, Cicadulini, Chiasmini, Deltocephalini, Macrostelini, Paralimnini, Eupelicini, Opsilini, Platymetopiini and Stenometopiini. The number of follicles is known for 18 species, 15 genera, and 6 tribes (the latter four tribes excepted). It varies from 5 in *Deltocephalus vulgaris* (Deltocephalini) and *Macrostelies cristatus* (Macrostelini) to 12 in *Artianus interstitialis* (Deltocephalini), with intermediate values from 6 to 9 per testes. In males of *Laburrus impictifrons* (Athysanini) from Poland, there are 8–9 follicles in each testis (Bednarczyk, 1983), but in males from Ukraine, 12 follicles per testis were recorded (Ivanov, 1926). The presence of 6 follicles is predominant, being found in 12 species from 11 genera and 6 tribes. Species of the same genus may have different numbers (e.g., 6 in *Deltocephalus pulicaris* but 5 in *D. vulgaris*, and 6 in *Macrosteles sexnotatus* but 5 in *M. cristatus*) or the same number (e.g., 6 in both *Doratura homophila* and *D. stylata*).

The number of ovarioles is known for 22 species, 22 genera, and 10 tribes. The number varies from 6 (occurring in 14 species, 14 genera, and 8 tribes) to 12 (2 species, 2 genera, all from the tribe Athysanini), with intermediate values of 7 (3 species, 3 genera, 2 tribes) and 8 (3 species, 3 genera, 3 tribes). As with follicles, the predominant number of ovarioles is 6 (in one ovary), which suggests that both 6 follicles and 6 ovarioles are characteristic of the entire subfamily Deltocephalinae. There are cases when the number of follicles and ovarioles in one species is the same, for example, 8 in *Cicadula quadripunctata* (Cicadulini) or 12 in *Artianus interstitialis* (Athysanini), but more often it is observed in species with the modal number of 6 (*Nephotettix cincticeps*, *Graminella nigrifrons*, *Balclutha brevis*, *Dalbulus maidis*, *Macrosteles sexnotatus* and *Psammotettix alienus*; tribes Chiasmini, Deltocephalini, Macrostelini and Paralimnini).

Eurymelinae. There are about 1,400 species in 180 genera and 11 tribes (Xue et al., 2020; Dmitriev et al., 2022). Data on follicles and/or ovarioles are available for 7 species (7 genera, tribes Idiocerini and Macropsini). The number of follicles is 6 per testis in all studied species, including *Oncopsis flavicollis* (Macropsini), collected in Ukraine (Ivanov, 1926), while males of this species collected in Poland have 3 follicles per testis (Bednarczyk, 1993). The number of ovarioles in the three studied species (three genera), on the contrary, varies quite considerably. This number is different in each species: 8 (per ovary) in *O. flavicollis* from Macropsini, 16–18 in *Idiocerus lituratus,* and 20–30 in *Rhytidorus nobilis* (Idiocerini).

Evacanthinae. There are about 653 species in 83 genera and 5 tribes (Dmitriev et al., 2022). Data are available only for *Evacanthus interruptus* (tribe Evacanthini), which has 6 follicles per testis and 6 ovarioles per ovary.

Ledrinae. There are about 333 species in 47 genera and 7 tribes (Dmitriev et al., 2022). Data are available for *Ledra aurita* and *Neotituria kongosana* (Ledrini), the females of which have 10–12 and 7 ovarioles per ovary, respectively.

Megophthalminae. There are 688 species worldwide belonging to 65 genera and 4 tribes (Bartlett et al., 2018; Dmitriev et al., 2022). Data on follicles and/or ovarioles are available for 15 species (9 genera, tribes Adelungiini and Agalliini). The testes studied in three species of Agalliini (genera *Agallia* Curtis, 1833 and *Anaceratagallia* Zachvatkin, 1946) have 6 follicles each. The number of ovarioles known to date in 13 species and 9 genera of both tribes varies widely: from 6 in all three studied species of the tribe Agalliini to 16 in two species of the tribe Adelungiini.

Typhlocybinae. There are approximately 5,000 species in 510 and 6 tribes (Bartlett et al., 2018; Dmitriev et al., 2022). Data on follicles and/or ovarioles are available for 18 species from 15 genera of the tribes Alebrini, Dikraneurini, Empoascini, Erythroneurini and Typhlocybini. Both testes and ovaries consist of a small number of elements, ranging from 2 to 5 in the case of follicles (studied in 14 species, 13 genera, 5 tribes) and from 3 to 6 (except 5) in the case of ovarioles (studied in 8 species, 6 genera, 3 tribes). Notably, males of 4 species (4 genera) of Typhlocybini have 3 follicles per testis, including males of *Edwardsiana lethierryi*, whereas another representative of this genus, *E. flavescens*, has 4 follicles per testis. All three studied species (3 genera) of Empoascini have 4 follicles in one testis. Three studied species of the tribe Erythroneurini have varying numbers of follicles: 2, 3 and 4. In the genus *Eupteryx* Curtis, 1829 (Typhlocybini), females of the *E. atropunctata* and *E. vittata* have 3 ovarioles per ovary, whereas females of *E. urticae* have 6 ovarioles.

Ulopinae. There are 139 species in 40 genera and 5 tribes (Bartlett et al., 2018; Dmitriev et al., 2022). Data are available for *Utecha trivia* (Ulopini), males of which have 4 follicles per testis.

Membracidae Rafinesque, 1815 is the largest treehopper family with 3,481 species in 431 genera, 45 tribes and 9 subfamilies (Bartlett et al., 2018; Dmitriev et al., 2022). Data on follicles and/or ovarioles are available for 6 species, 6 genera and three subfamilies, including Membracinae (2 species, 2 genera, 2 tribes), Centrotinae (3 species, 3 genera, 3 tribes) and Nicomiinae (1 species). The number of follicles varies from 4 (*Otinotus elongatus*, Centrotinae) to 14 (*Calloconophora argentipennis*, Membracinae), with intermediate values of 6 and 8. Different numbers are given for *Gargara genistae* collected in different regions: 6 for males from China (Tian et al., 2006) and 6–8 for males from Ukraine (Ivanov, 1926). The number of ovarioles in *Centrotus cornutus* (Centrotinae) and *Gargara genistae* (Membracinae) is 10–12 and 6 per ovary, respectively, with the latter species having the same number of ovarioles and follicles.

Myerslopiidae Evans, 1957 is a small family with 21 species and 3 genera in a single subfamily Myerslopiinae. This family is considered the basal membracoid family (Cryan, 2005; Cryan & Urban, 2012; Bartlett et al., 2018). In the only species studied, *Mapuchea chilensis*, three males studied had 6 follicles per testis, although the other two males studied showed some variation in the number of follicles in different testes.

CONCLUSIONS

In this paper, we assembled and analyzed all currently available data on the number of follicles in testes and the number of ovarioles in ovaries of Cicadomorpha. Currently, data on follicles are available for 103 species, 84 genera and 9 families of the superfamilies Cicadoidea (Tettigarctidae and Cicadidae), Cercopoidea (Aphrophoridae, Cercopidae and Ischnorhinidae) and Membracoidea (Aetalionidae, Cicadellidae, Membracidae and Myerslopiidae). Data on ovarioles are available for 65 species belonging to 56 genera of the same families, excluding Tettigarctidae, Aetalionidae, and Myerslopiidae. Overall, the available data cover no more than 0.4% of the species of Cicadomor-

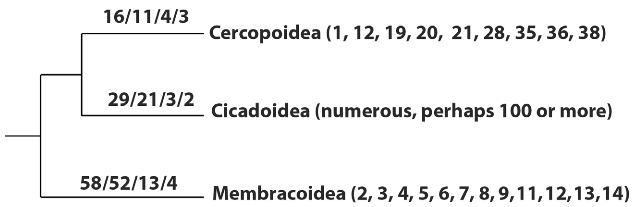

Fig. 1. The number of follicles (per testis) mapped on the phylogenetic tree of Cicadomorpha (according to Skinner et al., 2020). Numbers on branches indicate the number of species/genera/subfamilies/families studied. Numbers in parentheses indicate the number of follicles in a particular superfamily.

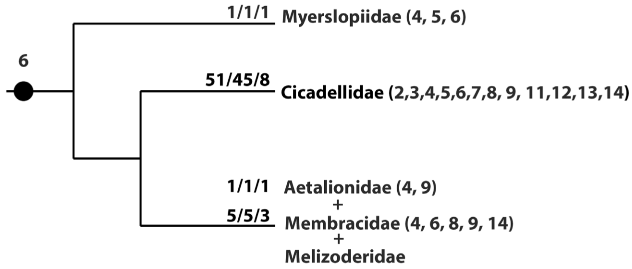

Fig. 2. The number of follicles (per testis) mapped on the phylogenetic tree of Membracoidea (according to Hu et al., 2022). Numbers on branches indicate the number of species/genera/subfamilies studied. Numbers in parentheses indicate the numbers of follicles in a particular family.

pha, with about 65% of them belonging to the superfamily Membracoidea, and even within the latter only about 0.4% of the species have been studied. In Cicadoidea and Cercopoidea, data are available for 1% and 0.7% of the described species, respectively. Although the available data are still very scarce, certain, albeit preliminary, conclusions can already be drawn.

Testes. In Cicadomorpha, the number of follicles varies widely: from 1 to "about 100 or more" per testis (Fig. 1, Table 2). As in Fulgoromorpha (Kuznetsova et al., 2024), in Cicadomorpha this trait is species-specific, usually stable at the level of closely related species and often, if variable, only fluctuates within small limits at higher taxonomic levels. Testes with one follicle in each have been reported in only one species (*Cercopis vulnerata*, Cercopidae, Cercopoidea), while testes with "about 100 or more" follicles in each are apparently characteristic of the entire superfamily Cicadoidea (Tables 1 and 2). In the sister superfamily Cercopoidea, the number of follicles varies in rather wide ranges. With the exception of *C. vulnerata*, all species studied to date have a relatively high number of follicles (though not as high as in Cicadoidea), typically 12 per testis or more. In most cases, the number is estimated by the authors as "many", "about 20" or a range is provided, e.g. 21–28, 28–35, or 36–38 follicles in the testis. The "many" estimate is widely used in Tian et al. (2006), and, judging from several figures presented in this paper (e.g., the testis of *Lepironina coleoptrata*, Aphrophoridae), these estimates suggest numbers somewhere around two dozen. Thus, both Cicadoidea and Cercopoidea are characterized by high numbers of follicles, with these numbers being much higher in the former.

However, in the case of Membracoidea the situation is quite different. There are considerably more data for this superfamily: 58 species, 52 genera and 4 families compared to 29 species, 21 genera, and 2 families in Cicadoidea, and 16 species, 11 genera, and 3 families in Cercopoidea. Therefore, it was expected that Membracoidea would exhibit more pronounced diversity, but this turned out not to be the case. In this superfamily, the number of follicles (in the testis) varies from 2 (in *Zyginidia viaduensis*, Cicadellidae) to 14 (in *Stroggylocephalus agrestis*, Membracidae), which is within noticeably narrower limits even in comparison with Cercopoidea, not to mention Cicadoidea. Six follicles is the most widespread number, occurring in 26 species (45% of those studied), 24 genera (59%) and three families (Cicadellidae, Membracidae, and Myerslopiidae) out of the four studied. Aetalionidae is the only family that does not exhibit this number, but just a single species, *Aetalion reticulatum*, has been studied. It can be assumed that 6 follicles per testis represents the ancestral state of this trait in Membracoidea (Fig. 2). This structure of testes has not been found in two other superfamilies of Cicadomorpha, but few data exist for them. On the other hand, testes with 6 follicles are predominant in Fulgoromorpha (Kuznetsova et al., 2024) and are considered as an ancestral state both in this infraorder and in Auchenorrhyncha as a whole (Emeljanov & Kuznetsova, 1983) (Fig. 3; see also below).

Ovaries. In Cicadomorpha, variability in the number of ovarioles appears to follow the same or similar pattern as in the follicles (Figs 4 and 5, Table 2). The lowest number of ovarioles per ovary is 3, which occurs in four species of Cicadellidae, including two species of the genus *Eupteryx* Curtis, 1829, while another species, *E. urticae,* has 6 ovarioles in the ovary. The highest numbers, predictably (given the high numbers of follicles in the testis), were found in Cicadoidea, in the family Cicadidae. In *Cicada orni*, each ovary contains 70–80 ovarioles (Dufour, 1833), while *Arunta perulata* has a much higher number of ovarioles, judging from the schematic representation of its ovary presented by Moulds (2005). This author suggested that high numbers of ovarioles are a characteristic feature of Cicadoidea. However, there are still limited data, and in any case, one species, *Cicadatra atra*, has only 6 ovarioles in the ovary (Table 1). This can be interpreted as an indication that such ovarian structure could be an ancestral

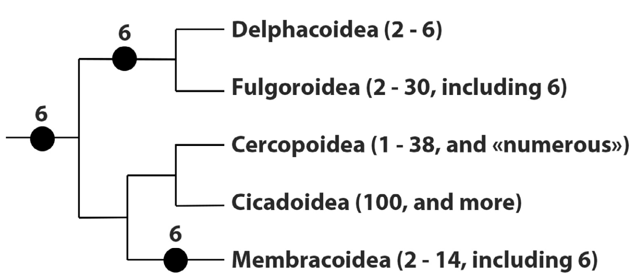

Fig. 3. The number of follicles (per testis) mapped on the phylogenetic tree of Auchenorrhyncha (according to Skinner et al., 2020) with indication of putative ancestral number. Numbers in parentheses indicate the numbers of follicles in a particular superfamily.

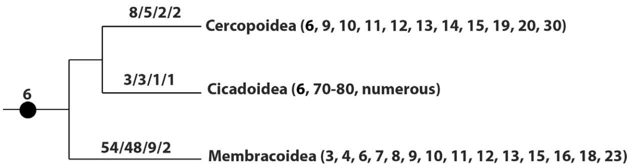

Fig. 4. The number of ovarioles (per ovary) mapped on the phylogenetic tree of Cicadomorpha (according to Skinner et al., 2020). Numbers on branches indicate the number of species/genera/subfamilies/families studied. Numbers in parentheses indicate the numbers of follicles in a particular superfamily.

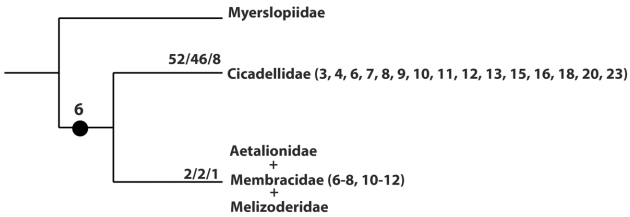

Fig. 5. The number of ovarioles (per ovary) mapped on the phylogenetic tree of Membracoidea (according to Hu et al., 2022). Numbers on branches indicate the number of species/genera/subfamilies studied. Numbers in parentheses indicate the numbers of ovarioles in a particular family.

characteristic also in Cicadidae, and that the high numbers observed arose secondarily in the evolution of the family. This conclusion aligns with the fact that the number 6 is most characteristic for both Cicadomorpha (present paper) and Fulgoromorpha (Kuznetsova et al., 2024) and is considered as evolutionarily primitive for Auchenorrhyncha as a whole (Emeljanov & Kuznetsova, 1983). Moreover, it is assumed that the number of ovarioles (as well as the number of follicles) in insects was initially low, in accordance with the number of pre-genital segments of the abdomen (Sharov, 1966). Another supporting argument is that where a species has the same number of follicles and ovarioles, this number is usually equal to 6. In contrast, when the numbers are high, they are always different (Table 1; see also above), thus confirming their independent origin.

It can be inferred that the number of ovarioles (as well as the number of follicles) is related to the size of the insect body, particularly the abdomen, i.e., the larger the insect, the more follicles and ovarioles it possesses. In some cases, such a correlation seems to be supported (e.g., Honěk, 1993; Tian et al., 2023), but in others it is not (e.g. Akingbohungbe, 1983). It is important to note that recent statistically sound analyses across different insect orders have shown that there is no generalized trade-off between body size and the number of ovarioles in insects (Church et al., 2021). Among Cicadomorpha, the smallest species (Typhlocybinae, Ulopinae) do indeed have few follicles (from 2 to 5 per testis) and ovarioles (4 or 6 per ovary), while relatively large species (Cicadoidea and Cercopoidea) have numerous follicles and ovarioles (Figs 1, 4, Table 1). The question of whether such a correlation actually exists in Auchenorrhyncha requires specific analysis.

As with follicles, most data on ovarioles are available for Membracoidea. A total of 54 species belonging to 48 genera of the families Cicadellidae and Membracidae

Table 2. The range of follicle and ovariole numbers in various taxa of Cicadomorpha.

Taxon	Number of studied species/genera/tribes)	Number of follicles per testis		Number of ovarioles per ovary	
		Variation range	Prevailing numbers	Variation range	Prevailing numbers
CICADOMORPHA	138/111/53	1–over 100	?	3 to 70–80	unclear
Cicadoidea	30/22/14	over 100	over 100	6, 70–80	unclear
Tettigarctidae	2/1/1	over 100	over 100	no data	no data
Cicadidae	28/21/13	over 100	over 100	6, 70–80	unclear
Cicadinae	16/11/10	over 100	over 100	6, 70–80	unclear
Cicadettinae	12/10/3	over 100	over 100	no data	no data
Cercopoidea	18/13/7	1–numerous*	unclear	6–30	unclear
Aphrophoridae	11/7/3	12–35	unclear	6–20	unclear
Cercopidae	6/5/2	1–numerous*	unclear	14–30	unclear
Cercopinae	3/2/2	1–numerous*	unclear	no data	no data
Cosmoscartinae	3/2/1	numerous*	unclear	no data	no data
Ischnorhinidae	1/1/1	36–38	unclear	no data	no data
Membracoidea	89/76/32	2–14	unclear	3–23	unclear
Aetalionidae	1/1/1	4, 9**	unclear	no data	no data
Cicadellidae	81/68/26	2–14	unclear	3–23	unclear
Aphrodinae	3/3/1	6–14	unclear	7	unclear
Cicadellinae	6/5/2	3–13	unclear	6	6
Deltocephalinae	28/25/10	6–12	6	6–12	6
Eurymelinae	7/7/2	3–6	6	8–23	unclear
Evacanthinae	1/1/1	6	unclear	6	unclear
Ledrinae	2/2/1	no data	no data	7–12	unclear
Megophthalminae	15/9/2	6	6	10–16	unclear
Typhlocibinae	18/15/5	2–5	4, 3	3–6	4, 3
Ulopinae	1/1/1	4	unclear	no data	no data
Membracidae	6/6/5	4–14	unclear	6–12	unclear
Membracinae	2/2/2	8–14	unclear	no data	no data
Centrotinae	3/3/3	4–8	unclear	6–12	unclear
Nicomiinae	1/1/1	8	unclear	no data	no data
Myerslopiidae	1/1	4–6**	unclear	no data	no data

* Exact number unknown. ** Different numbers in the species.

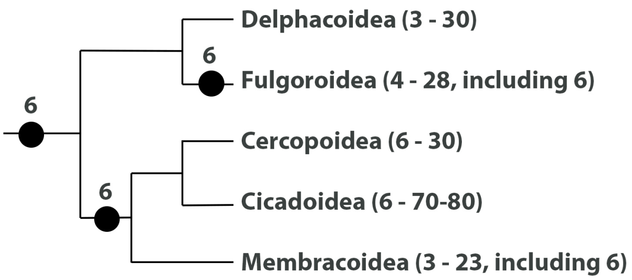

Fig. 6. The number of ovarioles (per ovary) mapped on the phylogenetic tree of Auchenorrhyncha (according to Skinner et al., 2020) with indication of putative ancestral number. Numbers in parentheses indicate the numbers of follicles in a particular superfamily.

were studied (Figs 4 and 5, Tables 1 and 2). The number of ovarioles ranges from 3 to 20–23 per ovary, with Cicadellidae exhibiting both values. Similar to follicles, the number 6 is clearly predominant, occurring in around 40% of species, 42% of genera and in both families studied. In Membracidae, data are available for only two species, with the number 6 mentioned for one of them, and only approximately. In Cicadellidae, however, it is found in 20 species (38.5% of those studied), 19 genera (41% of those studied) and in four of the seven subfamilies studied. This number is probably ancestral in Membracoidea, and possibly also in Cicadomorpha and Auchenorrhyncha as a whole (Fig. 6). If this hypothesis is accepted, it would appear that in Cicadoidea and Cercopoidea there is a tendency for the number of ovarioles to increase (although data are scarce, especially for the former), and in Membracoidea the ancestral number may either increase or decrease, although the increasing tendency seems to predominate.

In summary, since Emeljanov & Kuznetsova (1983) first argued that 6 follicles and 6 ovarioles were the primitive states of these traits in the evolution of Auchenorrhyncha, much more data have become available. Although data on both follicles and ovarioles are sparse and unevenly distributed within the suborder, it allows us to establish the polarity of these characters in the evolution of certain taxa: 6 follicles and 6 ovarioles are considered primitive, whereas the other values are regarded as derived (as discussed above).

Our analysis provides insight into the current state of knowledge regarding the structure of the testes and ovaries in Cicadomorpha and emphasizes the need for further data on additional species and higher taxa within this extensive group of hemipteroid insects.

ACKNOWLEDGEMENTS. The authors are grateful to A. Maryańska-Nadachowska for her help in collecting literature data. They also thank S. Grozeva and an anonymous reviewer for helpful comments on the manuscript. This work was performed within the framework of the State Research Project No. 122031100272-3.

AUTHOR CONTRIBUTIONS. Both authors have contributed equally to the MS (conceptualization, writing, review and editing). They also have read and agreed to the published version of the manuscript.

REFERENCES

Akingbohungbe A.E. 1983: Variation in testis follicle number in the Miridae (Hemiptera, Heteroptera) and its relationship to the higher classification of the family. — *Ann. Entomol. Soc. Am.* **76**: 37–43.

Ammar E.D. 1985: Internal morphology and ultrastructure of leafhoppers and planthoppers. In Nault L.R. & Rodriguez J.G. (eds): *The Leafhoppers and Planthoppers.* Wiley-Interscience, New York, pp. 127–162.

Araújo V.A., Bacca T. & Dias L.G. 2020: Estructura histológica del sistema reproductor masculino de la cigarrita *Aethalium reticulatum* (Hemiptera: Aethalionidae). — *Bol. Cient. Mus. Hist. Nat.* **24**: 127–137.

Bartlett C.R., Deitz L.L., Dmitriev D.A., Sanborn A.F., Soulier-Perkins A. & Wallace M.S. 2018: The diversity of the true hoppers (Hemiptera: Auchenorrhyncha). In Foottit R.G. & Adler P.H. (eds): *Insect Biodiversity: Science and Society, 2.* Wiley-Blackwell, Chichester, pp. 501–590.

Becker M. 1979: The nymphal stages and internal reproductive organs of *Macrosteles sexnotatus* (Fall.) (Hem. Cicadellidae). — *Entomol. Mon. Mag.* **115**: 11–16.

Bednarczyk J. 1983: Structure of the male reproductive system in *Alnetoidia alneti* (DHLB.) and *Populicerus populi* (L.) (Homoptera, Auchenorrhyncha). — *Acta. Biol. Katow.* **13**: 71–82.

Bednarczyk J. 1993: The structure of male reproductive system in species of the family Cicadellidae (Homoptera, Auchenorrhyncha). — *Acta Biol. Siles.* **22**: 126–143.

Chen J., Szwedo J., Wang B., Zheng Y., Jiang H., Jiang T., Wang X. & Zhang H. 2019a: A new bizarre cicadomorph family in mid-Cretaceous Burmese amber (Hemiptera, Clypeata). — *Cretac. Res.* **97**: 1–15.

Chen J., Wang B., Zheng Y., Jiang H., Jiang T., Bozdoğan H., Zhang J., An B., Wang X. & Zhang H. 2019b: Taxonomic review and phylogenetic inference elucidate the evolutionary history of Mesozoic Procercopidae, with new data from the Cretaceous Jehol Biota of NE China (Hemiptera, Cicadomorpha). — *J. Zool. Syst. Evol. Res.* **58**: 174–193.

Chen J., Zhang J., Liu W., Shah B., Dietrich C.H. & Duan Y. 2023: Morphological and ultrastructural studies of the internal reproductive systems of two deltocephaline leafhoppers, *Nephotettix cincticeps* and *Deltocephalus vulgaris* (Hemiptera, Cicadellidae, Deltocephalinae). — *ZooKeys* **1182**: 339–359.

Cheung W.W.K. 1994: Ultrastructural studies on the female reproductive system of the leafhopper *Euscelidium variegatus* Kirshbaum (Homoptera, Cicadellidae) I. The germarium. — *Cytologia* **59**: 93–101.

Church S.H., de Medeiros B.A.S., Donoughe S., Márquez Reyes N.L. & Extavour C.G. 2021: Repeated loss of variation in insect ovary morphology highlights the role of development in life-history evolution. — *Proc. R. Soc. (B)* **288**: 20210150, 9 pp.

Cryan J.R. 2005: Molecular phylogeny of Cicadomorpha (Insecta: Hemiptera: Cicadoidea, Cercopoidea and Membracoidea): adding evidence to the controversy. — *Syst. Entomol.* **30**: 563–574.

Cryan J.R. & Urban J.M. 2012: Higher-level phylogeny of the insect order Hemiptera: is Auchenorrhyncha really paraphyletic? — *Syst. Entomol.* **37**: 7–21.

Dietrich C.H. 2002: Evolution of Cicadomorpha (Insecta, Hemiptera). — *Denisia* **4**: 155–170.

Dietrich C.H. 2005: Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha). — *Fla Entomol.* **88**: 502–517.

Dietrich C.H., Allen J.M., Lemmon A.R., Lemmon E.M., Takiya D.M., Evangelista O., Walden K.K.O., Grady P.G.S. & Johnson K.P. 2017: Anchored hybrid enrichment-based phylogenomics of leafhoppers and treehoppers (Hemiptera: Cicadomorpha: Membracoidea). — *Insect Syst. Divers.* **1**: 57–72.

Dietrich C.H., Dmitriev D.A., Takiya D.M., Thomas M.J., Webb M.D., Zahniser J.N. & Zhang Y. 2022: Morphology-based phylogenetic analysis of Membracoidea (Hemiptera: Cicadomorpha) with placement of fossil taxa and description of a new subfamily. — *Insect Syst. Divers.* **6**: 1–30.

Dmitriev D.A., Anufriev G.A., Bartlett C.R., Blanco-Rodríguez E., Borodin O.I., Cao Y.-H., Deitz L.L., Dietrich C.H., Dmitrieva M.O., El-Sonbati S.A. et al. 2022: *World Auchenorrhyncha Database. TaxonPages.* URL: https://hoppers.speciesfile.org/ (last accessed 13 June 2024)

Dufour L. 1833: Recherches anatomiques et physiologiques sur les Hémiptères. — *Mém. Prés. Div. Sav. Acad. Sci. Inst. Fr.* **4**: 133–461.

Emeljanov A.F. & Kuznetsova V.G. 1983: The number of seminal follicles as a phylogenetic and taxonomic feature in the Dictyopharidae (Homoptera) and other leafhoppers. — *Zool. Zh.* **62**: 1583–1586 [in Russian, English abstract].

Emeljanov A.F., Golub N.V. & Kuznetsova V.G. 2001: Evolutionary transformation of testes and ovaries in booklice, birdlice, and sucking lice (Psocoptera, Phthiraptera: Mallophaga, Anoplura). — *Entomol. Rev.* **81**: 767–785.

Evangelista O., Tatarnic N. & Bayless K. 2024: Phylogenomics of endemic Australian Ulopinae (Hemiptera: Cicadomorpha: Cicadellidae). — *Invertebr. Syst.* **38**: IS23035, 19 pp.

Gadd G. 1910: To the comparative anatomy of cicadas and to the anatomy of *Tettigonia viridis* L. — *Russk. Entomol. Obozr.* **10**: 205–213 [in Russian, German abstract].

Gil-Fernandez C. & Black L.M. 1965: Some aspects of the internal anatomy of the leafhopper *Agallia constricta* (Homoptera: Cicadellidae). — *Ann. Entomol. Soc. Am.* **58**: 275–284.

Golub N.V., Kuznetsova V.G. & Rakitov R.A. 2014: First karyotype data on the family Myerslopiidae (Hemiptera, Auchenorrhyncha, Cicadomorpha). — *Comp. Cytogenet.* **8**: 293–300.

Grozeva S., Stoianova D., Konstantinov F., Simov N. & Kuznetsova V.G. 2022: A synopsis of the numbers of testicular follicles and ovarioles in true bugs (Heteroptera, Hemiptera) — sixty-five years of progress after J. Pendergrast's review. — *ZooKeys* **1136**: 71–123.

Hayashi F. & Kamimura Y. 2002: The potential for incorporation of male derived proteins into developing eggs in the leafhopper *Bothrogonia ferruginea*. — *J. Insect Physiol.* **48**: 153–159.

Helms T.J. 1968: Postembryonic reproductive systems development in *Empoasca fabae*. — *Ann. Entomol. Soc. Am.* **61**: 316–332.

Holmgren N. 1899: Beiträge zur Kenntniss der weiblichen Geschlechtsorgane der Cicadarien. — *Zool. Jb. Abt. Syst. Geogr. Biol. Tiere* **12**: 403–410.

Honěk A. 1993: Intraspecific variation in body size and fecundity in insects: A general relationship. — *Oikos* **66**: 483–492.

Hu Y., Dietrich C.H., Skinner R.K. & Zhang Y. 2022: Phylogeny of Membracoidea (Hemiptera: Auchenorrhyncha) based on transcriptome data. — *Syst. Entomol.* **48**: 97–110.

Hummel N.A., Zalom F.G. & Peng C.Y.S. 2006: Anatomy and histology of reproductive organs of female *Homalodisca coagulata* (Hemiptera, Cicadellidae, Proconiini), with special emphasis on categorization of vitellogenic oocytes. — *Ann. Entomol. Soc. Am.* **99**: 920–932.

Ivanov S.P. 1926: To the knowledge of the sexual apparatus of Homoptera Cicadoidea. — *Russk. Entomol. Obozr*. **20**: 210–227 [in Russian].

Kaplin V.G. 1985: Number of ovarioles and size of eggs in arid cicadines (Homoptera, Cicadinea). — *Zool. Zh.* **64**: 1743–1745 [in Russian, English abstract].

Kuznetsova V.G & Kirillova V.I. 1993: Karyotype and male internal reproductive system of *Aetalion reticulatum* L. (Aetalionidae, Cicadelloidea, Cicadina): phylogenetic aspects. — *Beitr. Entomol.* **43**: 119–122.

Kuznetsova V.G., Nokkala S. & Shcherbakov D.E. 2002: Karyotype, reproductive organs, and pattern of gametogenesis in *Zorotypus hubbardi* Caudell (Insecta: Zoraptera, Zorotypidae), with discussion on relationships of the order. — *Can. J. Zool.* **80**: 1047–1054.

Kuznetsova V.G., Labina E.S., Shapoval N.A., Maryańska-Nadachowska A. & Lukhtanov V.A. 2012: *Cacopsylla fraudatrix* sp. n. (Hemiptera: Psylloidea) recognised from testis structure and mitochondrial gene *COI*. — *Zootaxa* **3547**: 55–63.

Kuznetsova V.G., Maryańska-Nadachowska A., Khabiev G.N., Karagyan G. & Krivokhatsky V.A. 2019: Variation in the number of testicular follicles and ovarioles among 18 lacewing species of the families Myrmeleontidae, Ascalaphidae, and Nemopteridae (Insecta, Neuroptera, Myrmeleontiformia). — *ZooKeys* **894**: 33–51.

Kuznetsova V.G., Golub N.V. & Maryańska-Nadachowska A. 2024: Number of seminal follicles and ovarioles in Fulgoromorpha (Hemiptera: Auchenorrhyncha): variability and evolutionary trends. — *Eur. J. Entomol.* **121**: 109–123.

Lachowska-Cierlik D., Maryańska-Nadachowska A., Kuznetsova V. & Picker M. 2015: First chromosomal study of Mantophasmatodea: karyotype of *Karoophasma biedouwense* (Austrophasmatidae). — *Eur. J. Entomol.* **112**: 599–605.

Lupa B., Kim J.K. & Bilinski S.M. 1999: The ovary of *Neotituria kongosana* (Hemiptera, Cicadomorpha: Ledridae). Ultrastructure of the tropharium and terminal filament. — *Folia Biol. (Kraków)* **47**: 123–130.

Maryańska-Nadachowska A., Kuznetsova V.G. & Taylor G.S. 2001a: Meiotic karyotypes and structure of testes in males of 12 species of Psyllidae: Acizzinae, Carsidaridae and Triozidae (Hemiptera: Psylloidea) from Australia. — *Aust. J. Entomol*. **40**: 357–364.

Maryańska-Nadachowska A., Taylor G.S. & Kuznetsova V.G. 2001b: Meiotic karyotypes and structure of testes in males of 17 species of Psyllidae: Spondyliaspidinae (Hemiptera: Psylloidea) from Australia. — *Aust. J. Entomol*. **40**: 349–356.

Maryańska-Nadachowska A., Kuznetsova V.G. & Abdul-Nur H. 2008: A chromosomal study on a Lebanese spittle bug *Philaenus arslani* (Hemiptera: Auchenorrhyncha: Aphrophoridae). — *Eur. J. Entomol.* **105**: 205–210.

Mishra R.K. 1979: Male reproductive organs of five species of Auchenorrhyncha Homoptera. — *Acta Entomol. Bohemoslov.* **76**: 162–168.

Moulds M.S. 2005: An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. — *Rec. Aust. Mus.* **57**: 375–446.

Özyurt Koçakoğlu N., Candan S. & Arslan H. 2024a: Anatomical and histological structures of the male reproductive system of adult *Cercopis vulnerata* Rossi, 1807 (Hemiptera: Cercopidae). — *Biologia* **79**: 155–160.

Özyurt Koçakoğlu N., Candan S. & Arslan H. 2024b: Notes on the female reproductive system of the red-and-black froghopper, *Cercopis vulnerata* Rossi, 1807 (Hemiptera: Cercopidae) – light and electron microscopy studies. — *Acta Zool.* **105**: 253–261.

Pappalardo A.M., D'Urso V., Viscuso R., Ferrito V., Giunta M.C., Cupani S. & Vitale D.G.M. 2016: Morphostructural investigation of the female reproductive system and molecular evidence for *Wolbachia* in *Balclutha brevis* Lindberg 1954 (Hemiptera, Cicadellidae). — *Micron* **81**: 23–33.

Silva S.M. 2022: *Morfologia do sistema reprodutor masculino e dos espermatozoides de duas espécies de Membracidae (Hemiptera: Auchenorrhyncha)*. MSc thesis, Universidade Federal de Viçosa, Viçosa, vi + 35 pp. [in Portuguese, English abstract].

Skinner R.K., Dietrich C.H., Walden K.K.O., Gordon E., Sweet A.D., Podsiadlowski L., Petersen M., Simon C., Takiya D.M. & Johnson K.P. 2020: Phylogenomics of Auchenorrhyncha (Insecta: Hemiptera) using transcriptomes: examining controversial relationships via degeneracy coding and interrogation of gene conflict. — *Syst. Entomol*. **45**: 85–113.

Sodré R.F., Coelho L.B.N., Rezende P.H., Costa D.A., Dias G. & Lino-Neto J. 2024: Morphology of the male reproductive system and spermatozoa of *Mahanarva fimbriolata* (Stål, 1854) (Hemiptera: Cercopidae) with evidence of a spermatostyle in the sperm conjugation. — *Micron* **178**: 103591, 7 pp.

Song N., Cai W. & Li H. 2017: Deep-level phylogeny of Cicadomorpha inferred from mitochondrial genomes sequenced by NGS. — *Sci. Rep.* **7**, 10429, 11 pp.

Su M., Dietrich C.H., Zhang Y.L. & Dai W. 2014: Ultrastructure of the spermatozoa of *Psammotettix striatus* (Linnaeus) and *Exitianus nanus* (Distant) (Hemiptera, Auchenorrhyncha, Cicadellidae, Deltocephalinae). — *Arthropod Struct. Dev.* **43**: 559–570.

Sharov A.G. 1966: *Basic Arthropodan Stock with Special Reference to Insects*. Pergamon Press, Oxford, London, 271 pp.

Szwedo J. 2018: The unity, diversity and conformity of bugs (Hemiptera) through time. — *Earth Environ. Sci. Trans. R. Soc. Edinb*. **107**: 109–128.

Tian R.G., Yuan F. & Zhang Y.L. 2006: Male reproductive system and spermatogenesis in Homoptera (Insecta, Hemiptera). — *Entomotaxonomia* **28**: 241–253.

Tian L., Wang X., Wang Y., Gu X., Li X., An S., Yin X. & Bai S. 2023: rearing host dependency of ovariole number and body size in *Campoletis chlorideae* Uchida (Hymenoptera: Ichneumonidae). — *Insects* **14**: 483, 14 pp.

Tsai J.H. & Perrier J.L. 1996: Morphology of the digestive and reproductive systems of *Dalbulus maidis* and *Graminella nigrifrons* (Homoptera: Cicadellidae). — *Fla Entomol.* **79**: 563–578.

Vitale D.G.M., Viscuso R., D'Urso V., Gibilras S., Sardella A., Marletta A. & Pappalardo A.M. 2015: Morphostructural analysis of the male reproductive system and DNA barcoding in *Balclutha brevis* Lindberg 1954 (Homoptera, Cicadellidae). — *Micron* **79**: 36–45.

Xue Q., Dietrich C.H. & Zhang Y. 2020: Phylogeny and classification of the leafhopper subfamily Eurymelinae (Hemiptera: Cicadellidae) inferred from molecules and morphology. — *Syst. Entomol.* **45**: 687–702.

Zhang B.B., Zhang C.N., Dietrich C. & Dai W. 2016: Anatomy and ultrastructure of male reproductive system in two leafhoppers *Cicadella viridis* and *Kolla paulula* (Hemiptera, Auchenorrhyncha, Cicadellidae). — *Ann. Entomol. Soc. Am.* **109**: 447–462.

Received June 18, 2024; revised and accepted October 16, 2024
Published online November 20, 2024