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REVIEW

Number of seminal follicles and ovarioles in Fulgoromorpha (Hemiptera: Auchenorrhyncha): Variability and evolutionary trends

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Abstract. In this paper data on the number of follicles in testes and the number of ovarioles in ovaries of planthoppers (Hemiptera: Fulgoromorpha) are summarised and discussed. Fulgoromorpha include about 14,000 described species belonging to 21 families distributed throughout the world. The number of follicles is known for 186 species, 123 genera and 17 families, and the number of ovarioles is known for 52 species, 44 genera and 11 families. Almost 80% of the species studied belong to the families Dictyopharidae, Delphacidae, Issidae, Cixiidae and Achilidae. The number of follicles per testis and ovarioles per ovary varies within similar ranges, from 2 to 30 and from 3 to just over 30, respectively. The predominant number of follicles is 6, which is found in more than one third of the species and in almost all of the families studied. This number is considered as an ancestral trait for Fulgoromorpha. In each family, the ancestral number can vary both upwards or downwards, probably due to either polymerization or oligomerization. In the more basal families, a decreasing trend clearly predominates, whereas an increasing trend predominates in the more advanced families. As for the numbers of ovarioles, they tend to vary within families, with rare exceptions (e.g., Dictyopharidae), but that is probably due to the lack of data.

INTRODUCTION

The hemipteran suborders Fulgoromorpha Evans, 1946 and Cicadomorpha Evans, 1946 (often considered as infraorders), together comprising Auchenorrhyncha, a group now known to be paraphyletic, are two highly diverse, ecologically and agriculturally important groups with more than 43,000 species in 33 recent families (Cryan & Urban, 2012; Bartlett et al., 2018; Skinner et al., 2020). They are widely distributed and constitute the main component of the herbivorous fauna of terrestrial ecosystems on all continents (except Antarctica). Cicadomorpha include 5 recent superfamilies: Cicadoidea, Cercopoidea, Membracoidea, Cicadelloidea and Myerslopioidea (Szwedo, 2018). Fulgoromorpha, commonly named planthoppers, have more than 14,000 described species distributed among about 20 families, depending on the classification used (Bartlett et al., 2018; Bucher et al., 2023; Bourgoin, 2024). According to a recently proposed classification (Bourgoin & Szwedo, 2022, 2023), Fulgoromorpha include two recent superfamilies: Delphacoidea (with the families Cixiidae and Delphacidae) and Fulgoroidea (other families). Planthoppers are very mobile insects with many dispersing over great distances; they feed almost exclusively on plants (some feed on fungal hyphae, at least in the larval stage). Planthoppers are mostly monophagous or narrowly oligophagous and are major vectors of pathogens causing serious plant diseases (Skinner et al., 2020 and references therein).

There are many studies on the internal reproductive organs in insects (see review books: Matsuda, 1976; Büning, 1994; Chapman, 2013; Klowden, 2013). They show that in different groups of insects, the reproductive organs of males and females, respectively, are characterized by a similar general morphology, but differ markedly in the number of seminal follicles (tubes in which the initial diploid spermatogonia develop to haploid spermatozoa) in the testes, and ovarioles (tubes containing developing eggs) in the ovaries. These numbers vary considerably in Insecta in general, but their variation is sometimes poorly understood in evolutionary terms. In males, the number of follicles can vary from one per testis, e.g., in some psyllids (Hemiptera: Psylloidea) (Maryańska-Nadachowska et al., 2001) and true bugs (Hemiptera: Heteroptera) (Grozeva et al., 2022), to several tens or even hundreds per testis in some Hymenoptera (Chapman, 2013). The number of follicles is usually constant and the same in both testes of a male (at least in cases of low numbers). Many higher-level taxa are characterized by an invariant or nearly invariant

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number of follicles. For example, about two-thirds of psyllids have two follicles per testis but some subfamilies of the families Carsidaridae (Carsidarinae) and Aphalaridae (Rhinocolinae, Spondyliaspidinae) are characterized by one follicle per testis (Głowacka et al., 1995; Maryańska-Nadachowska et al., 2001). In true bugs, about half of the species studied have 7 follicles per testis, but available data for the more studied families show different and constant numbers of follicles at the level of tribes and sometimes subfamilies (Grozeva et al., 2022). The most common numbers in most insects appear to range from 4 to 10 per testis (Kuznetsova et al., 2019).

In females, the number of ovarioles can vary from one per ovary, e.g., in some aphids (Hemiptera: Aphidoidea) (Michalik et al., 2013), to about 400 in some coccids (Hemiptera: Coccoidea) (Ramírez-Cruz et al., 2008) and even more than 1,000 in some groups; in general, the number of ovarioles in insects varies by at least four orders of magnitude (Church et al., 2021). The most common number of ovarioles ranges from 4 to 10 per ovary (Klowden, 2013) and thus coincides with the most common follicle numbers in males (Kuznetsova et al., 2019). The number of ovarioles is largely species-specific, but can show significant intraspecific and interspecific variation due to various factors such as, for example, differences in ecology or a particular lifestyle (Kaplin, 1985; Taylor & Whitman, 2010; Faille & Pluot-Sigwalt, 2015). For example, in aphids, variation in ovariole number has been shown to be associated with mixed reproductive strategies (Michalik et al., 2013). Variability in ovariole number in insects has been the subject of numerous studies, notably in *Drosophila* Fallén, 1823 (for a review, see Green, 2014). In *D. melanogaster* Meigen, 1830, there are latitudinal clines in the number of ovarioles (Schmidt et al., 2005), indicating the influence of natural selection (Lobell et al., 2017). To identify evolutionary patterns in changes of ovariole number in insects, Church et al. (2021) collected information on the numbers of ovarioles in 2,103 species and analysed their phylogenetic distribution across 28 orders and 301 families. The authors concluded that the evolution of this trait included a series of transitions between variable and invariant states, with several independent lineages with an almost complete absence of variation in the number of ovarioles. Note in this regard that quite a few insects show stable numbers of ovarioles in taxa at different levels. For example, 7 ovarioles per ovary is characteristic of true bugs of the family Miridae (Grozeva et al., 2022); 10 ovarioles is the only known value so far in neuropterans of the suborder Myrmeleontiformia (Kuznetsova et al., 2019); 4 ovarioles are found in almost all Lepidoptera (Church et al., 2021); in Coleoptera, many higher taxa have characteristic numbers (Scholtz, 1990).

Information on the number of ovarioles is more often used to address questions related to insect development, life cycles, reproductive biology and evolution (e.g., Klowden, 2013). Follicle number appears to be an informative trait for phylogenetic considerations and systematics of insects at different levels in the taxonomic hierarchy (e.g., Emeljanov & Kuznetsova, 1983; Maryańska-Nadachowska et al., 2001; Ferreira et al., 2004; Wieczorek, 2006; Barcellos et al., 2015; Grozeva et al., 2022).

The internal anatomy of planthoppers has been investigated for nearly two centuries. The first reports were published by Dufour (1833), Apgar (1887) and Holmgren (1899) followed shortly by Kershaw & Kirkaldy (1910), Gadd (1910, 1914) and Ivanov (1926, 1928). With the exception of a few species studied by Kershaw & Kirkaldy (1910) and Ivanov (1928), all of these early studies were on Cicadomorpha. Until the 1990s, studies were sporadic (e.g., Fennah, 1950; O'Brien, 1971; Mochida, 1973) and then interest in the problem increased significantly and dozens of papers were published on both Fulgoromorpha and Cicadomorpha. The general organization of the reproductive systems of males and females in different auchenorrhynchan species is similar, except for some important details, primarily the number of follicles and ovarioles, although also the shape and location of seminal vesicles, and the number, shape and location of accessory glands (e.g., Backus, 1985; Kirillova, 1989; D'Urso et al., 2005). Males have two testes each with a different number of follicles, two different ducts that join to form the median common duct, seminal vesicles where sperm is stored, accessory glands that synthesize proteins and a median ejaculatory duct (Fig. 1a). Females have a pair of ovaries with varying numbers of ovarioles, a pair of lateral oviducts, the spermatheca responsible for the reception, storage and release of sperm to fertilize eggs, copulatory bursa and a vagina; accessory glands may also be present (Fig. 1b). The ovaries are of the meroistic telotrophic type, in which nurse cells accompany oocytes (Büning, 1994; Biliński, 1998).

In 1983, Emeljanov and Kuznetsova published a review of the data available at that time on the number of follicles and ovarioles in Auchenorrhyncha. In general, literature and their own data on 59 species, 42 genera and 11 families (7 from Fulgoromorpha and 4 from Cicadomorpha) are summarized and briefly discussed, with special emphasis on the fulgoroid family Dictyopharidae. These authors outlined trends in the evolutionary transformations of the number of follicles and ovarioles in Auchenorrhyncha, primarily in Dictyopharidae. Later, Kuznetsova et al. (1998) published new data on the number of seminal follicles in 37 species from 24 genera and 7 families of Fulgoromorpha and briefly discussed all available data on these families at that time. Although by the late 1990s much data had already been obtained for many other families of both Fulgoromorpha and Cicadomorpha, not only on seminal follicles but also on ovarioles (e.g. Kaplin, 1985; Kuznetsova, 1986; Kirillova, 1989; Kuznetsova & Kirillova, 1990; Bednarczyk, 1993; Kuznetsova et al., 1998), a comprehensive review of the available literature has not been attempted. In addition, many original articles on the internal reproductive organs of males and females of Auchenorrhyncha, both Fulgoromorpha (e.g., Tian et al., 2004; D'Urso et al., 2005; Maryańska-Nadachowska et al., 2006, 2016; Kuznetsova et al., 2009; Liu & Qin, 2020) and Cicadomorpha (e.g., Golub et al., 2014; Zhang et al., 2016; Araújo et al., 2020),

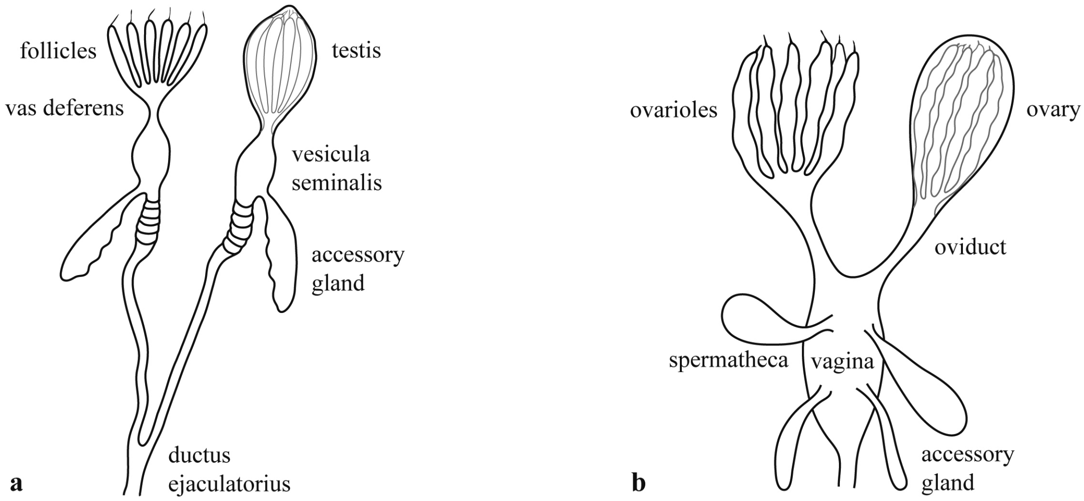

Fig. 1. Schematic view of the male (a) and female (b) reproductive systems of Fulgoromorpha.

have appeared over the past few decades. Currently, the number of species studied with respect to the structure of testes and ovaries in Fulgoromorpha and Cicadomorpha has almost tripled and it seems appropriate to publish an updated list.

All the information available to date will be presented in two articles. This article focuses on Fulgoromorpha. Table 1 (at the end of the article) lists all the species studied in relation to the number of follicles and ovarioles. Species are distributed by genera, tribes and subfamilies within the corresponding families. The classification of Fulgoromorpha and the number of species and genera in each family follow in most cases Bourgoin (2024). To provide an evolutionary context for the results, the states of the studied characters were mapped onto Bartlett's 2020 phylogenetic tree of Fulgoromorpha. On this tree, the number of species and genera studied, the ranges of variability in follicle and ovariole numbers and the most characteristic numbers for the 17 families, for which data are available, are presented (Fig. 2). In the Conclusions, the diversity of the analysed traits is briefly evaluated and the main trends in their evolution in Fulgoromorpha identified. It is hoped that this review has implications for future studies on the reproductive morphology in Fulgoromorpha and Auchenorrhyncha in general and that the use of data on the structure of testes and ovaries may provide additional information for understanding relationships between planthopper taxa.

MATERIAL AND METHODS

This review is part of a long-term research project on the morphology of the reproductive system, cytogenetics and evolution of the order Hemiptera (see recent reviews: Gavrilov-Zimin et al., 2021; Kuznetsova et al., 2021; Grozeva et al., 2022; Aguin-Pombo & Kuznetsova, 2023). Data collected over the years on the structure of the testes and ovaries of planthoppers (Fulgoromorpha) in terms of the number of seminal follicles and ovarioles now constitute a significant proportion of all the currently available similar data on Auchenorrhyncha as a whole. Planthoppers were collected during the authors' expeditions (1986–2021) or provided by colleagues. The material came from different regions of the Palaearctic (Europe, Central Asia, Oriental and South-Oriental regions), the Nearctic (North America), the Neotropical realm (Central and South America, Cuba) and the Afrotropical realm (Western, Central, and South Africa). Species identification was carried out mainly by A.F. Emeljanov and V.M. Gnezdilov. Voucher specimens are stored in the insect collection of the Zoological Institute of RAS, St. Petersburg.

RESULTS AND DISCUSSION

As stated in the Introduction, Fulgoromorpha include about 14,000 species in 21 extant families and two superfamilies: Delphacoidea, with 2 families and Fulgoroidea, with 19 families (Bourgoin, 2024). Data on the number of follicles and ovarioles in planthoppers were compiled from a thorough literature review; new authors' data on 9 species, 6 genera and 7 families are also added. In total, information is currently available for 17 families (132 genera, 200 species and subspecies); data are completely lacking for the small families Achilixiidae and Eurybrachidae, and for two African families, Gengidae and Hypochthonellidae, in each of which only a few species are known. Comments on the data for each family are given below.

Superfamily Delphacoidea

Cixiidae Spinola, 1839 is the largest planthopper family, with 2,640 species (18.6% of the currently known planthopper species) in 254 genera and three subfamilies: Borystheninae, Bothriocerinae and the large cosmopolitan subfamily Cixiinae. This family is considered the most basal of the extant lineages of Fulgoromorpha (Bartlett, 2020; Bourgoin, 2024). Data are available for two species of Bothriocerinae (the genus *Bothriocera* Burmeister, 1835) and 14 species of Cixiinae (12 genera, 6 tribes). In Cixiinae, the number of follicles is very variable and may differ even in closely related species, e.g., 4 follicles per testis in *Cixius borussicus* and 5 in *C. cunicularius*. Numbers of 3, 4, 5 and 6 are found in this subfamily. The latter value is characteristic of the tribe Pentastirini, in which four out of the five species studied have 6 follicles per testis, which is considered the plesiomorphic condition of the testis in Fulgoromorpha (Emeljanov & Kuznetsova, 1983). Males of *Hyalesthes obsoletus* have 3 follicles per testis

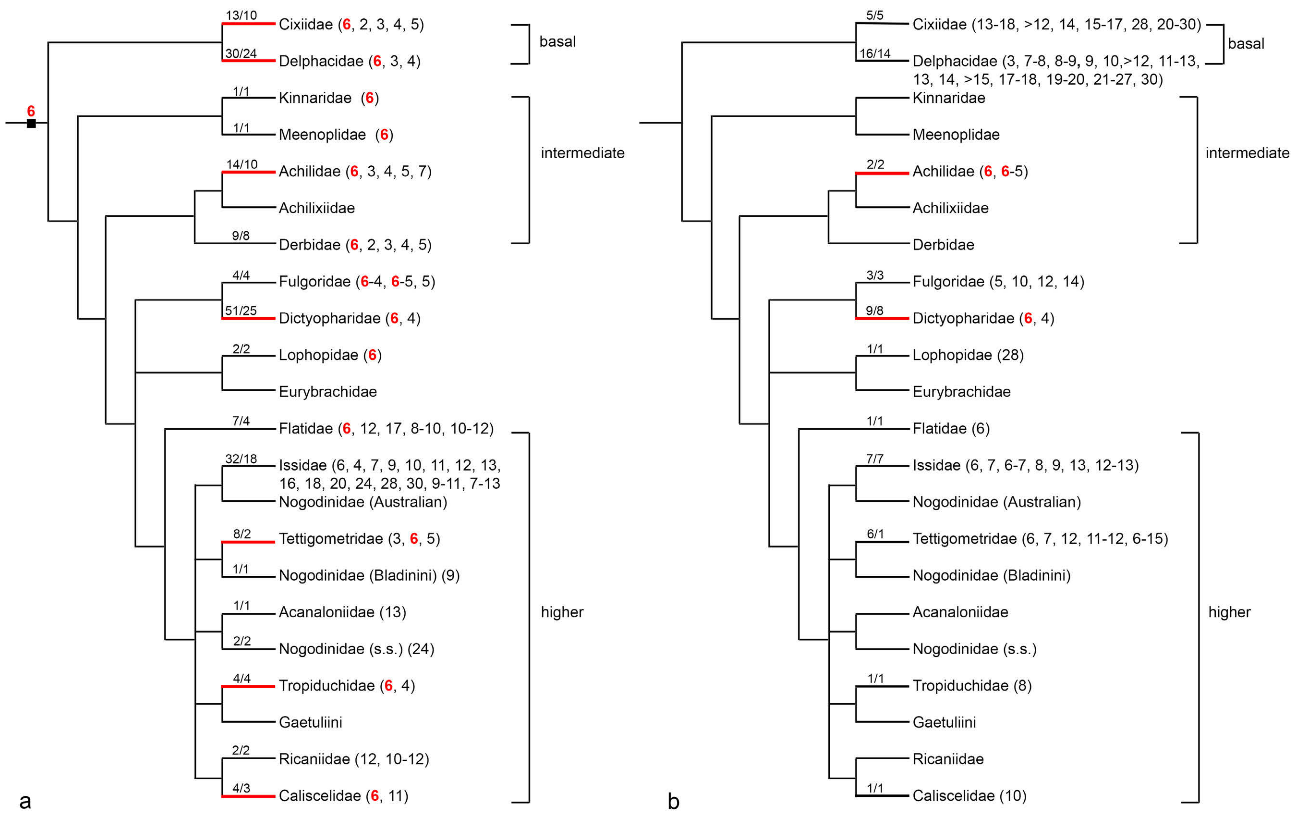

Fig. 2. Numbers of seminal follicles (a) and ovarioles (b) mapped on a phylogenetic tree of Fulgoromorpha (Bartlett, 2020). The numbers on the branches indicate the number of species (numerator) and genera (denominator) studied. Numbers in parentheses refer to the numbers of follicles and ovarioles in a particular family. Numbers in bold red font indicate the inferred ancestral number(s) of follicles and ovarioles in different families and in Fulgoromorpha as a whole. Numbers hyphenated denote the range in variation in the number of follicles and/or ovarioles in a species.

(new data). In Bothriocerinae, both species of *Bothriocera* have 2 follicles per testis (the smallest number recorded in Fulgoromorpha). The number of ovarioles is known for 5 species from 5 genera of Cixiinae. The numbers are relatively high, exceeding 12 (per ovary) in all species, and in most cases varying, e.g., from 12 to 18 in *Cixius nervosus*, from 20 to 30 in *Pentastridius leporinus* and from 15 to 17 in *Demetia irrorata.*

Delphacidae Leach, 1815 is the second largest family of planthoppers, with 2,236 species and 428 genera in 6 subfamilies. Delphacidae are considered to be the basal family of Fulgoromorpha and phylogenetically close to Cixiidae (Bartlett, 2020; Skinner et al., 2020; Bourgoin, 2024). Data on testes and/or ovarioles are available for 37 species, 28 genera and 3 subfamilies: Asiracinae (2 species, 2 genera), Delphacinae (34 species, 25 genera, 4 tribes) and Stenocraninae (*Stenocranus major*). Testes consisting of 3 follicles are predominant and found in all the species studied, except three. The exceptions are both of the species studied of the basal subfamily Asiracinae, *Asiraca clavicornis* and *Copicerus irroratus*, as well as *Metropis* sp. of Delphacinae, which have 6 follicles per testis. Kirillova (1989) analysed the distribution of follicle numbers in Delphacidae in comparison with the families Dictyopharidae and Tettigometridae. The conclusion was that the initial number in the evolution of Delphacidae was 6 and the number 3 is derived, thus confirming the hypothesis that the number of follicles tends to decrease during the evolution of Fulgoromorpha (Emeljanov & Kuznetsova, 1983). Unlike the number of follicles, the number of ovarioles is very variable and often differs in the right and left ovary of the same female; in most cases, the number of ovarioles is approximate. In general, the number of ovarioles in delphacids varies from 3 in *Tropidocephala tuberipennis* (Tropidocephalini) to more than 30 in the genus *Delphax* Fabricius, 1798 (Delphacini), which is the highest number recorded in planthoppers.

Superfamily Fulgoroidea

Acanaloniidae Amyot & Audinet-Serville, 1843 is a very small family, with 94 species and 7 genera in one subfamily and one tribe distributed in the New World (Bourgoin, 2024). Acanaloniidae was previously included as a subfamily Acanaloniinae in the Issidae, but is now treated separately (Urban & Cryan, 2007; Skinner et al., 2020). The testes of the only species studied, *Acanalonia bivittata*, contain 13 follicles each (like in *Issus lauri* of Issidae).

Achilidae Stål, 1866 is a moderately numerous family, with 521 species in 162 genera and three subfamilies: Apatesoninae, Achilinae, and Myconinae (Bartlett et al., 2018; Bourgoin, 2024). Data are available on the number of follicles in 14 species in 10 genera of the subfamily Achilinae (tribes Plectoderini, Seviini, and Achilini). In general, their numbers vary from 3 to 7 per testis. The most characteristic are 6 and 3, which occur at similar frequencies in almost half of the species and genera studied; but both these numbers occur in *Catonia* Uhler, 1895 and *Plectoderes* Spinola, 1839. Only females of *Catonia sanctaeluciae* (Plectoderini) and *Cixidia sikaniae* (Achilini) have been studied. In both cases, the number of ovarioles coincides with the number of follicles (6 in both cases). The testis consisting of 6 follicles and the ovary consisting of 6 ovarioles are considered to be the initial state in the evolution of the family, at least of the subfamily Achilinae (Kuznetsova et al., 1998).

Caliscelidae Amyot & Audinet-Serville, 1843 is a small family of about 253 species and 80 genera in two subfamilies: Caliscelinae and Ommatidiotinae (Bourgoin, 2024). Data are available for 4 species (3 genera in both subfamilies). In Caliscelinae, both of the species studied in the genus *Caliscelis* de Laporte, 1833 have 6 follicles per testis. In Ommatidiotinae, *Ommatidiotus dissimilis* and *Adenissus riadicus* have 6 and 11 follicles, respectively. The number 6 is accepted as the ancestral state of this trait in this family (Maryańska-Nadachowska et al., 2006), although it is based on data for very few species. Females of *Ommatidiotus dissimilis* have 10 ovarioles per ovary.

Derbidae Spinola, 1839 includes 1,722 species in 166 genera and 3 subfamilies: Breddiniolinae, Derbinae and Otiocerinae (Bourgoin, 2024), which makes it the third most species-rich family of planthoppers (after Cixiidae and Delphacidae). Data on ovary structure are absent; there are data on the structure of testes, though few (9 species from 8 genera), for each of the subfamilies. The number of follicles per testis varies from 2 to 6, including all 5 possible values. In the basal subfamily Breddiniolinae, both species of the genus *Cedusa* Fowler, 1904 have 5 follicles and *Malenia sicula* has 6 follicles per testis. In the subfamily Derbinae, *Vekunta* sp. has 6 follicles and three other species have 4 follicles per testis. In the subfamily Otiocerinae, the two species studied, *Diostrombus politus* (Zoraidini) and *Muiralevu quadrimaculatus* (Rhotanini), have 3 and 2 follicles per testis, respectively. The discovery of 6 follicles per testis in *Malenia sicula* (new data) from the basal subfamily Breddiniolinae supports the hypothesis that this number is ancestral for this family (Kuznetsova et al., 1998).

Dictyopharidae Spinola, 1839 is a relatively large family, with 748 species in 160 genera and two subfamilies: the diverse and cosmopolitan Dictyopharinae (551 species, 121 genera and subgenera within 13 tribes) and the xerophilic Orgeriinae (191 species, 35 genera and subgenera within 4 tribes) occurring only in arid regions of the Holarctic (Emeljanov, 1991; Bourgoin, 2024). Dictyopharidae are the most extensively studied planthoppers in terms of follicle number (Issidae are second). In total, data are available for 52 species in 26 genera of both Dictyopharinae (tribes Nersiini, Dictyopharini, Orthopagini, Scolopini) and Orgeriinae (tribes Ranissini, Almanini, Orgeriini) (Kuznetsova, 1986; Kuznetsova et al., 2009). All of the species of Dictyopharinae studied (18 species, 9 genera, all 4 tribes) have 6 follicles per testis. In Orgeriinae, the same pattern is observed in all of the species studied in the basal tribe Ranissini (9 species, 4 genera) as well as in all those in the tribe Orgeriini (3 species, 2 genera). The tribe Almanini differs from the two previous tribes in that each of the 21 species studied (11 genera) has testes with 4 follicles. Data on the number of ovarioles, although very few, are available for both subfamilies and for three tribes of Orgeriinae. In Dictyopharinae, the only species studied, *Dictyophara europaea* (Dictyopharini), has 6 ovaries per ovary. In Orgeriinae, the only species studied in the tribe Ranissini, *Ranissus scythe*, also has 6 ovarioles per ovary; in the tribe Almanini, all 5 species studied (5 genera) have 4 ovarioles per ovary; in the tribe Orgeriini, the two species studied (2 genera) have 6 ovarioles per ovary. It is noteworthy that in all species in which the numbers of both follicles and ovarioles are known, the numbers are the same, indicating a parallel evolution of these structures in Dictyopharidae. The number 6 is regarded as the ancestral state of testes and ovaries in Dictyopharidae, from which testes and ovaries of Almanini were thought to have evolved. The tribes Orgeriini and Almanini are the most advanced taxa within Orgeriinae (Emeljanov, 1980), so, the structure of the gonads in Orgeriini may indicate the secondary appearance of an ancestral trait in this tribe (Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986; Kuznetsova et al., 2009).

Flatidae Spinola, 1839 is the fourth largest family of planthoppers (after Cixiidae, Delphacidae and Derbidae), with 1,457 species in 300 genera and two subfamilies distributed worldwide (Bourgoin, 2024). Data on the number of follicles and ovarioles are available only for the subfamily Flatinae, tribes Poekilopterini (2 species, 1 genus) and Flatini (6 species, 4 genera). In the monogeneric tribe Poekilopterini, the two species of the genus *Poekiloptera* Latreille, 1796 studied have 12 and 17 follicles per testis, respectively. In the second tribe, the two species of the genus *Phantia* Fieber, 1866 studied and *Salurnis marginella* have 6 follicles per testis, a number considered evolutionarily basal for Fulgoromorpha (Emeljanov & Kuznetsova, 1983). In two species of the genus *Ormenis* Stål, 1862, the number of follicles varies from 8 to 10 and from 10 to 12 per testis, respectively. In *Phylliana serva* (Flatini), the only species in which females have been studied, there are 12 ovarioles in each ovary.

Fulgoridae Latreille, 1807 is a large family, with 769 species in 142 genera and 8 subfamilies, especially abundant and diverse in the tropics (Bourgoin, 2024). There is very little relevant information on this family, but some is available for 4 subfamilies: Strongylodematinae (1 species, Capocleini), Fulgorinae (1 species, Laternariini), Dichopterinae (1 species, Dorysarthrini), and Aphaeninae (1 species, Aphainini, and 1 species, Limoisini). In all species, males have 6 follicles in each testis, although in the two males studied in *Capocles podlipaevi* the number of follicles varies between testes (Kuznetsova et al., 2009). It can be assumed that the number 6 is ancestral for the family as a whole. The number of ovarioles varies: 5 per ovary in *Dorysarthrus sumakowi* (Dichopterinae), 10 in *Pyrops candelaria* (Fulgorinae), 12 and 14 in different populations of *Lycorma delicatula* (Aphaeninae).

Issidae Spinola, 1839 is one of the largest and most diverse families of planthoppers, with 1,099 described species in 223 genera (Bourgoin, 2024); it is considered to be the closest group to the base of the monophyletic so-called "higher" Fulgoroidea (Bartlett, 2020). The family includes 2 subfamilies: Issinae and Hysteropterinae (Gnezdilov et al., 2022). Issidae is one of the most studied planthopper families (after Dictyopharidae and Delphacidae) with respect to the structure of the testes and, although to a much lesser extent, also of the ovaries. Data on the number of follicles and/or ovarioles are available for 30 species in 17 genera of Hysteropterinae and for 3 species in 2 genera of Issinae. The number of follicles varies from 4 in *Palmallorcus punctulatus* and 6 in *Scorlupella discolor* to 30 in *Zopherisca skaloula* in Hysteropterinae. Significant variability in the number of follicles in taxa of different ranks is recorded. For example, each of the three species studied in the genus *Palmallorcus* Gnezdilov, 2003 has a different number per testis: 4, 10 and 9–11. The genus *Zopherisca* Emeljanov, 2001 has the highest numbers in this family, 24 in *Z. penelopae*, 28 in *Z. tendinosa tendinosa* and 30 in *Z. scaluola*. The status of the latter was elevated from subspecies (*Z. tendinosa scaluola*), based on differences in follicle number (Kuznetsova et al., 2010). *Kervillea basiniger* and *K. scoleogramma*, belonging to the subgenus *Kervillea* Bergevin, 1918, have 10 and 12 follicles per testis, respectively. In the genus *Mycterodus* Spinola, 1839, *M. colossicus* and *M. pallens* (subgenus *Semirodus* Dlabola, 1987) have 18 follicles per testis, whereas *M. etruscus* and *M. intricatus* (subgenus *Mycterodus*) have 16 and 20 follicles per testis, respectively. It should be noted that specimens of *Issus coleoptratus* (Issinae) from Ukraine and France have 20 follicles, whereas those from Spain have 13 follicles per testis. In the same genus, *I. lauri* has 13 follicles, and *Latissus dilatatus* 12 follicles per testis. Thus, the number of follicles is taxonomically informative at both the generic and species level. In some genera, the number of follicles is constant. For example, three species in the genus *Bubastia* Emeljanov, 1975 and two species in the genus *Hysteropterum* Amyot & Audinet-Serville, 1843 have 10 follicles per testis. Two species in the genus *Agalmatium* Emeljanov, 1971 have 11 follicles per testis. Based on the available data, the number 10 per testis seems to be the most typical for the family Issidae, at least for the subfamily Hysteropterinae, as it is recorded in almost half of the species studied and in more than half of the genera studied. Two hypotheses are proposed. According to one, intensive processes of follicle number increasing occur in Issidae, with a fixed number of 10 at the subfamily level (Maryańska-Nadachowska et al., 2006). According to the other hypothesis, the number 10 is a plesiomorphic trait for this group, and higher numbers or, less frequently, lower numbers are apomorphic traits (Kuznetsova et al., 2010). Further studies are needed to determine the basal number of follicles in Issidae. Regardless of whether the number of follicles in the closest ancestor of the family was 10 or still 6, it can be stated that in the evolution of Issidae the tendency for increasing of the number of follicles prevailed. The number of ovarioles is known for 7 species in 7 genera of both subfamilies. It varies within fairly narrow limits, from 6 per ovary in *Tingissus guadarramense* and *Brachyprosopa umnovi* (Hysteropterinae) to 13 in *Issus lauri* (Issinae), and there is no apparent trend in the variability in the number.

Kinnaridae Muir, 1925 is a small family, with only 116 species and 25 genera in two subfamilies: Kinnarinae and Prosotropinae, both distributed predominantly in the tropics and subtropics (Bourgoin, 2024). The only species studied, *Oeclidius* pr. *nanus* (Kinnarinae), has 6 follicles per testis.

Lophopidae (Stål, 1866) is a small family, with 175 species and 49 genera in two subfamilies: Lophopinae and Menoscinae (Bourgoin, 2024). One species has been studied in each subfamily. In the first, *Pyrilla perpusilla* has testes each with 6 follicles and ovaries each with 28 ovarioles; in the second, males of *Elasmoscelis trimaculata* have 6 follicles per testis.

Meenoplidae Fieber, 1872 is a small family, with 169 species and 23 genera in two subfamilies: Meenoplinae and Kermesiinae (Bourgoin, 2024). The only species studied, *Nisia carolinensis* (Meenoplinae), has 6 follicles per testis and there is no information on ovaries.

Nogodinidae Melichar, 1898 is a medium-sized family, with 378 species in 99 genera and 4 subfamilies: Nogodininae, Colpopterinae, Gastriniinae and Bladininae (Gnezdilov, 2017; Bourgoin, 2024). Nogodinidae are repeatedly found to be paraphyletic in various phylogenies; they appear as a polyphyletic grouping separated by genera occupying different positions within the "higher" planthoppers (Bartlett, 2020; Skinner et al., 2020; Bucher et al., 2023 and Fig. 2). Information on follicles is available for only 3 species, of which one belongs to the monogeneric subfamily Bladininae, tribe Bladinini (*Bladina mimica cymula*, 9 follicles per testis) and the other two to the largest subfamily Nogodininae, tribes Nogodinini (*Biolleyana pictifrons*) and Pisachini (*Pisacha* sp.), both with 24 follicles per testis; there is no information on ovaries.

Ricaniidae Amyot & Audinet-Serville, 1843 is one of the relatively large families, with 444 species, 71 genera and two subfamilies distributed worldwide, mainly in the tropics (Bourgoin, 2024). Data on follicles are available for two species in the subfamily Ricaniinae: *Ricania speculum* with 12 follicles per testis and *Orosanga japonica*, in which the number varies from 10 to 12, with 11 predominating (Kuznetsova & Kirillova, 1990); there is no information on ovaries.

Tettigometridae Germar, 1821 is a small family, with 88 species, 14 genera and 4 subfamilies: Nototettigometrinae, Tettigometrinae, Egropinae and Phalixinae (Bourgoin, 2024). Data are available for 8 species and 2 genera: *Nototettigometra patruelis* (Nototettigometrinae), the testes of which consist of 3 follicles each, and 7 species of the genus *Tettigometra* Latreille, 1804 in the most species-rich subfamily Tettigometrinae. This genus is subdivided into 8 subgenera. In five species belonging to the subgenera *Mitricephalus* Signoret, 1866 and *Tettigometra* Latreille, 1804, and in *Tettigometra atra* (unknown subgenus), there are 6 follicles in each testis. In *T. costulata*, which belongs to the monotypic subgenus *Stirometra* Emeljanov, 1980, there are 5 follicles in each testis, but one of the five males examined has 5 and 6 follicles in its testes. Although data are scarce, the number 6 is considered evolutionarily basal for the family as a whole (Kuznetsova & Kirillova, 1990). The reduced number of follicles in *T. costulata* agrees well with the notion that the subgenus *Stirometra* is more advanced than other subgenera of *Tettigometra* (Emeljanov, 1980). In contrast to testes, ovaries are characterized by a highly variable number of ovarioles, at least in *Tettigometra*. The number varies in different species (12 in *T. obliqua*, 7 in *T. varia* and 6 in *T. costulata*), in different females (in *T. vitellina*) and between different ovaries in the same female (in *T. eremi*).

Tropiduchidae Stål, 1866 is an intermediate-sized family, with 682 species in 197 genera and two subfamilies, Tropiduchinae and Elicinae, which are most diverse in humid tropics. Data are available for 4 species (4 genera, 2 tribes) of Tropiduchinae. In the tribe Tambiniini, both of the species studied have 6 follicles per testis. In the tribe Cyphoceratopini, *Achilorma bicincta* also has 6 follicles per testis and *Numicia viridis* has 4 follicles per testis and 8 ovarioles per ovary. The ancestor of Tropiduchidae apparently had six follicles per testis (Kuznetsova et al., 1998).

CONCLUSIONS

In this paper the number of follicles was analysed in 186 species belonging to 123 genera and 17 planthopper families and the number of ovarioles was analysed in 52 species belonging to 44 genera and 11 planthopper families (excluding Acanaloniidae, Derbidae, Kinnaridae, Meenoplidae, Nogodinidae and Ricaniidae, for which there is no information on ovarioles) (Table 1 and Fig. 2; for phylogenetic relationships, see Bartlett, 2020). The data collected on the number of follicles and ovarioles give a good picture of the current stage of development in this field. The review revealed that the number of follicles and ovarioles in planthoppers is highly variable. The number of follicles (in a testis) varies from 2 (in two species of Cixiidae and one species of Derbidae) to 30 (in one species of Issidae). An analysis of this wide range in the number of follicles revealed trends in taxa of different ranks, especially in families for which there are relatively large amounts of information, such as Dictyopharidae, Delphacidae, Issidae, Cixiidae and to a lesser extent Achilidae, Caliscelidae, Derbidae, Fulgoridae and Tettigometridae.

This analysis revealed that the number of follicles is a species-specific trait in Fulgoromorpha, usually stable within species and often invariant at higher taxonomic levels. The predominant numbers are 6, 4 and 3. Six follicles per testis, the modal number in Fulgoromorpha, are recorded in 72 species (38%), 46 genera (38%) and 14 families, including the basal families Cixiidae and Delphacidae. In the three families, in which number 6 is not recorded, very few species have been studied (3 species in Nogodinidae, 2 in Ricaniidae and 1 in Acanaloniidae). Four follicles per testis are recorded for 33 species (18%), 19 genera (16%) and 7 families, including Cixiidae and Delphacidae, but mainly in the family Dictyopharidae, in which it is the second number after 6. Three follicles per testis are recorded for 35 species (18%), 29 genera (23%) and 4 families, but most frequently in Delphacidae and Achilidae. Numbers below or above these values are reported in various families, but usually rarely. The exception is the family Issidae, in which the number 10 predominates along with other higher numbers (11 to 30), although four of the 33 species studied have fewer follicles, including 6 in *Scorlupella discolor* (Hysteropterinae). The number 10 is considered to be a possible plesiomorphic trait for the family (Kuznetsova et al., 2010). If this hypothesis is accepted, then the number 6 is a derived character state in the Issidae.

The number of ovarioles (in an ovary) varies from 3 (in one species of Delphacidae) to about 30 (in one species of Cixiidae) and even more than 30 (in one species of Delphacidae). There is very little information (one or two species) in most families. There is slightly more information for the families Delphacidae (16 species, 14 genera), Dictyopharidae (9 species, 8 genera), Issidae (7 species, 7 genera) and Cixiidae (5 species, 5 genera). In contrast to follicles, the number of ovarioles is very variable even at the species level, especially in the case of high numbers (more than 10), and there are some examples of variability in closely related species. This is particularly evident in the large genus *Tettigometra* (Tettigometridae), in which each of the six species studied has a different number of ovarioles, whereas, in contrast, the number of follicles is 6 per testis in all these species. It is noteworthy, however, that in the family Dictyopharidae the number of ovarioles is stable at the level of subfamilies and tribes and coincides with the number of follicles, and the changes in these characters are associated with the evolution of the family (Kuznetsova, 1986; Kuznetsova et al., 2009). Another family in which the number of ovarioles is the same as the number of follicles is Achilidae, but very little information is currently available for this family.

The basic number of follicles and ovarioles in insects is believed to be 7 (Emeljanov & Kuznetsova, 1983), which is the number of pregenital segments in females (Sharov, 1966). A recent ancestral reconstruction of testes and ovaries in true bugs (Heteroptera) shows that 7 follicles per testis and 7 ovarioles per ovary are ancestral states for this suborder (Grozeva et al., 2022). However, Heteroptera appear to be the only suborder of Hemiptera that has retained ancestral numbers across lineages, whereas other higher taxa of Hemiptera are dominated by lower numbers (for a review, see Emeljanov & Kuznetsova, 1983; see also Maryańska-Nadachowska et al., 2001; Wieczorek et al., 2019). The above applies to the number of follicles, as the number of ovarioles in these groups can vary very widely; for example, the ovary of scale insects (Coccoidea) can contain up to 200 ovarioles (Szklarzewicz et al., 2010). In Fulgoromorpha, the number 7 is characteristic neither for testes or ovaries as only in *Synecdoche helenae* (Achilidae), there are 7 follicles per testis, and only in *Tshurtshurnella pythia* (Issidae), does each ovary consist of 7 ovarioles.

As shown above, 6 follicles per testis is definitely the most characteristic case in planthoppers, which confirms the hypothesis put forward previously that this is the most likely ancestral state in Fulgoromorpha (Emeljanov & Kuznetsova, 1983). The inferred ancestral number varies upwards or downwards in various families, which is probably due to either polymerization or oligomerization. Based on morphology, fossil records and DNA nucleotide sequences, Fulgoromorpha are divided into three clades: "basal", "intermediate" and 'higher" (Urban & Cryan, 2007; Bartlett et al., 2018; Bartlett, 2020). Mapping of follicle numbers on the phylogenetic tree of Fulgoromorpha (Fig. 2a) showed that in the basal families, Cixiidae and Delphacidae (Delphacoidea), and "intermediate" families, the ancestral number of 6 tends to decrease, which is particularly noticeable in the better-studied families Achilidae, Derbidae and especially Dictyopharidae. In the "higher" families, at least in the best-studied family Issidae, and in Flatidae and Nogodinidae s. str., there is a general tendency for the number of follicles to increase. It is noteworthy that in the family Tettigometridae, whose phylogenetic relationships with other planthopper families has been the subject of debate for many years (see Mozaffarian et al., 2018 for references and discussion), the trend is a decrease in the number of follicles, but this is based on very limited information.

Compared to follicles, the number of ovarioles in planthoppers is characterized by a greater variability, including intraspecific and intraindividual variation. In some cases, when different numbers are given for a species in the original publication, this may be the result of an error in counting ovarioles in an individual, especially if there are many ovarioles. In addition, as noted in the Introduction, the number of ovarioles in females may vary depending on biological or environmental factors. However, in the family Dictyopharidae, the number of ovarioles is stable in individual females, species and higher taxa. There are other examples in the literature where the number of ovarioles is invariant or nearly invariant in higher-level insect taxa (see Introduction). It can be assumed that the number of ovarioles in planthoppers, despite the variability, is also a species-specific trait, like the number of seminal follicles, and is determined genetically. In the opinion of the authors, much work remains to be done in order to clarify the problem and test this and other hypotheses.

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Table 1. The number of testicular follicles and ovarioles in 17 families of Fulgoromorpha.

Taxa	Locality	Number of follicles per testis	Number of ovarioles per ovary	References
DELPHACOIDEA				
1. CIXIIDAE				
Bothriocerinae				
1. *Bothriocera tinealis* Burmeister, 1835	Brazil	2	–	Kuznetsova et al., 1998
2. *Bothriocera* sp.	Panama	2	–	Kuznetsova et al., 1998
Cixiinae				
Andini				
3. *Andes hemina* Fennah, 1978	Vietnam	3	–	New data
Oecleini				
4. *Mundopa kotoshonis* Matsumura, 1914	Taiwan	4	14	Kuznetsova et al., 1998
Cixiini				
5. *Cixius* (*Orinocixius*) *borussicus* Wagner, 1939	Russia	4	–	Kuznetsova & Kirillova, 1990
6. *C.* (*Ceratocixius*) *cuncularius* (Linnaeus, 1767)	Russia	5	–	Kuznetsova et al., 1998
7. *C.* (*Cixius*) *nervosus* (Linnaeus, 1758)	Ukraine Poland	– –	13–18 Over 12	Kirillova, 1989; Szklarzewicz et al., 2007
8. *C.* (*Sciocixius*) *stigmaticus* (Germar, 1818)	Ukraine	4	–	Kirillova, 1989
Duilini				
9. *Duilius* sp.	Kazakhstan	4	–	Kuznetsova & Kirillova, 1990: as *Hemitropis* sp.
Pentastirini				
10. *Eumecurus abyssinicus* (Van Stalle, 1987)	Ethiopia	6	–	Kirillova, 1993
11. *Hyalesthes obsoletus* Signoret, 1865	Russia	3	–	New data
12. *Melanoliarus* sp.	Cuba	6	–	Kuznetsova & Kirillova, 1990
13. *Norialsus* sp.	South Africa	6	–	New data
14. *Pentastridius* (*Pentastridius*) *leporinus* (Linnaeus, 1761)	Ukraine	6	20–30	Ivanov, 1928: as *Oliarius leporinus* Linnaeus, 1762
Pintaliini				
15. *Cubana tortrix* Uhler, 1895	Lesser Antilles, Saint Lucia	–	28	Fennah, 1948
16. *Demetia irrorata* (Uhler, 1895)	Lesser Antilles, Saint Vincent	–	15–17	Fennah, 1948: as *Cubanella irrorata* (Uhler, 1895)
2. DELPHACIDAE				
Asiracinae				
Asiracini				
17. *Asiraca clavicornis* (Fabricius, 1794)	Kyrgyzstan	6	19–20	Kirillova, 1989
18. *Copicerus irroratus* Swartz, 1802	Cuba	6	19–20	Kirillova, 1989; Kuznetsova & Kirillova, 1990
Delphacinae				
Delphacini				
19. *Conomelus anceps* (Germar, 1821)	Poland	–	Over 12	Szklarzewicz et al., 2007
20. *Chloriona unicolor* (Herrich-Schäffer, 1835)	Finland	3	13	Lindberg, 1939
21. *Criomorphus albomarginatus* Curtis, 1833	Unknown	3	–	Kirillova, 1989
22. *C. williamsi* China, 1939	Unknown	3	–	Kirillova, 1989
23. *Delphax* sp.1	Ukraine	–	Over 30	Ivanov, 1928
24. *Delphax* sp.2	Ukraine	–	10	Kirillova, 1989
25. *Delphacinus mesomelas* (Boheman, 1850)	Unknown	3	–	Kirillova, 1989
26. *Dicranotropis* (*Dicranotropis*) *hamata* (Boheman, 1847)	Ukraine	3	Over 15	Kirillova, 1989
27. *Euconomelus lepidus* (Boheman, 1847)	Russia Unknown	3 3	7–8 –	Emeljanov & Kuznetsova, 1983; Kirillova, 1989
28. *Eurybregma* (*Eurybregma*) *nigrolineata* Scott, 1875	Unknown	3	–	Kirillova, 1989
29. *Javesella* (*Javesella*) *dubia* (Kirschbaum, 1868)	Unknown	3	–	Kirillova, 1989
30. *J.* (*J.*) *forcipata* (Boheman, 1847)	Ukraine Unknown	3 3	– –	Kirillova, 1989: as *Delphax forcipata* (Boheman, 1847); Kirillova, 1989
31. *J.* (*J.*) *obscurella* (Boheman, 1847)	Unknown	3	–	Kirillova, 1989
32. *J.* (*J.*) *pellucida* (Fabricius, 1794)	Poland Japan Unknown	– 3 3	Over 12 17–18 –	Szklarzewicz et al., 2007; Mochida, 1973; Kirillova, 1989
33. *J.* (*Haffnerianella*) *stali* (Metcalf, 1943)	Ukraine	3	Over 12	Kirillova, 1989: as *Delphax bohemani* Stal, 1854
34. *Kosswigianella denticauda* (Boheman, 1847)	Unknown	3	–	Kirillova, 1989: as *Acanthodelphax denticaudus* (Boheman, 1847)
35. *Megamelus scutellaris* Berg, 1883	Argentina	–	11–13	Mattison et al., 2017
36. *M. notulus* (Germar, 1830)	Unknown	3	–	Kirillova, 1989
37. *Metropis* sp.	Tajikistan	6	–	Kuznetsova & Kirillova, 1990
38. *Muellerianella brevipennis* (Boheman, 1847)	Unknown	3	–	Kirillova, 1989
39. *Laodelphax striatellus* (Fallén, 1826)	Ukraine	3	–	Ivanov 1928: as *Delphax striatella* (Fallén, 1826)
40. *Nilaparvata lugens* (Stål, 1854)	Japan Japan	– 3	21–27 –	Chen et al., 1979; Mochida & Okada 1979
41. *Peregrinus maidis* (Ashmead, 1890)	USA	3	–	Backus, 1985
42. *Ribautodelphax albostriata* (Fieber, 1866)	Unknown	3	–	Kirillova, 1989
43. *R. pungens* (Ribaut, 1953)	Unknown	3	–	Kirillova, 1989
44. *Sogatella furcifera* (Horváth, 1899)	Far East of Russia, Primorsky Krai	3	–	Kuznetsova & Kirillova, 1990
45. *Tagosodes orizicolus* (Muir, 1926)	USA, Louisiana	3	14	McMillian, 1963: as *Sogata orizicola* (Muir, 1926)
46. *Stobaera muiri* Kramer, 1974	Cuba	–	8–9	Kuznetsova & Kirillova, 1990
47. *Struebingianella lugubrina* (Boheman, 1847)	Unknown	3	–	Kirillova, 1989
48. *Xanthodelphax straminea* (Stål, 1858)	Unknown	3	–	Kirillova, 1989

Kelisiini				
49. *Kelisia guttula* (Germar, 1818)	Sweden	–	9	Holmgren, 1899: as *Stenocarenus guttula* (Germar, 1818)
50. *K. praecox* Haupt, 1935	Unknown	3	–	Kirillova, 1989
Tropidocephalini				
51. *Tropidocephala tuberipennis* (Mulsant & Rey, 1855)	Greece	–	3	New data
Saccharosydnini				
52. *Saccharosydne procerus* Matsumura, 1931	Unknown	3	–	Kirillova, 1989
Stenocraninae				
53. *Stenocranus major* (Kirschbaum, 1868)	Unknown	3	–	Kirillova, 1989
FULGOROIDEA				
3. ACANALONIIDAE				
54. *Acanalonia bivittata* (Say, 1825)	USA	13	–	Maryańska-Nadachowska et al., 2006
4. ACHILIDAE				
Achilinae				
Plectoderini				
55. *Amblycratus pallidus* Uhler, 1895	Lesser Antilles, Saint Lucia	6	–	Fennah, 1950
56. *Amblysellus* sp.	Brazil	3	–	Kuznetsova et al., 1998
57. *Catonia sanctaeluciae* Fennah, 1950	Lesser Antilles, Saint Lucia	6	6	Fennah, 1950
58. *Catonia* sp.	Brazil	3	–	Kuznetsova et al., 1998
59. *Deferunda* sp.	Vietnam	3	–	Kuznetsova et al., 1998
60. *Juniperthia indella* (Ball, 1933)	USA	3	–	O'Brien, 1971: as *Juniperia indella* Ball, 1933
61. *Momar maculifrons* (Van Duzee, 1912)	USA	5	–	O'Brien, 1971
62. *Plectoderes* sp. 1	Brazil	4	–	Kuznetsova et al., 1998
63. *Plectoderes* sp. 2	Brazil	3	–	Kuznetsova et al., 1998
64. *Plectoderes* sp. 3	Brazil	6	–	Kuznetsova et al., 1998
65. *Synecdoche helenae* (Van Duzee, 1918)	USA	7	–	O'Brien, 1971
Seviini				
66. *Sevia* sp. 1	Brazil	6	–	Kuznetsova et al., 1998
67. *Sevia* sp. 2	Brazil	6	–	Kuznetsova et al., 1998
Achilini				
68. *Cixidia sikaniae* D'Urso & Guglielmino, 1995	Italy	6	6 (occasionally 5)	D'Urso et al., 2005
5. CALISCELIDAE				
Caliscellinae				
Caliscelini				
69. *Caliscelis* (*Caliscelis*) *bonellii* (Latreille, 1807)	Spain France	6 6	– –	Maryańska-Nadachowska et al., 2006; New data
70. *C.* (*Melanero*) *nero* Fennah, 1967	South Africa	6	–	Maryańska-Nadachowska et al., 2006
Ommatidiotionae				
Adenissini				
71. *Adenissus riadicus* Dlabola, 1985	United Arab Emirates, Sharijah Desert Park	11	–	New data
72. *Ommatidiotus dissimilis* (Fallén, 1806)	Ukraine	6	10	Kirillova, 1989
6. DERBIDAE				
Breddiniolinae				
Cedusini				
73. *Cedusa* sp. 1	Brazil	5	–	Kuznetsova et al., 1998
74. *Cedusa* sp. 2	Mexico	5	–	Kuznetsova et al., 1998
75. *Malenia sicula* Haupt, 1924	Italy	6	–	New data
Derbinae				
Derbini				
76. *Mysidia* sp.	Brazil	4	–	Kuznetsova et al., 1998
Cenchreini				
77. *Omolicna cubana* (Myers, 1926)	Cuba	4	–	Kuznetsova et al., 1998
78. *Persis* (*Persis*) *stali* Muir, 1918	Brazil	4	–	Kuznetsova et al., 1998
79. *Vekunta* sp.	Vietnam	6	–	Kuznetsova et al., 1998
Otiocerinae				
Rhotanini				
80. *Muiralevu quadrimaculatus* (Muir, 1915)	Taiwan	2	–	Kuznetsova et al., 1998: as *Formolevu quadrimaculatus* (Muir, 1915)
Zoraidini				
81. *Diostrombus politus* Uhler, 1896	Vietnam	3	–	Kuznetsova et al., 1998
7. DICTYOPHARIDAE				
Dictyopharinae				
Nersiini				
82. *Hyalodictyon taurinum* (Stål, 1862)	French Guyana	6	–	Kuznetsova et al., 2009
83. *Rhynchomitra cubanensis* (Melichar, 1912)	Cuba	6	–	Kuznetsova & Kirillova, 1990: as *Rh. cubana* (Melichar, 1912)
84. *Trimedia* cf. *viridata* (Stål, 1862)	French Guyana	6	–	Kuznetsova et al., 2009
Dictyopharini				
85. *Callodictya krueperi* (Fieber, 1872)	Bulgaria	6	–	Kuznetsova et al., 2009
86. *Dictyophara* (*Chanithus*) *avocetta* Oshanin, 1879	Kazakhstan	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
87. *D.* (*Ch.*) *pannonica* (Germar, 1830)	Ukraine	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
88. *D.* (*Ch.*) *scolopax* Oshanin, 1879	Kazakhstan	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986

89. *D.* (*Dictyophara*) *europaea* (Linnaeus 1767)	Ukraine Ukraine	6 6	6 –	Kirillova, 1989; Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
90. *D.* (*Euthremma*) *multireticulata* Mulsant & Rey, 1855	Ukraine	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
91. *D. nekkana* Matsumura, 1940	Mongolia	6	–	Kuznetsova, 1986: as *Dictyophara kaszabi* Dlabola, 1967
92. *Philoteria* sp.	Guinea	6	–	Kuznetsova & Kirillova, 1990
93. *Raivuna pallida* (Donovan, 1800)	India	6	–	Bhattacharya & Manna, 1973: as *Dictyophara pallida* Donovan, 1800
94. *R. striata* (Oshanin, 1879)	Kazakhstan	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
Orthopagini				
95. *Saigona ussuriensis* (Lethierry, 1878)	Far East of Russia, Primorsky Krai	6	–	Kuznetsova, 1986
96. *Saigona* sp.	China	6	–	Tian et al., 2004
Scoloptini				
97. *Scolops abnormis* Ball, 1902	USA, California	6	–	Kuznetsova et al., 2009
98. *S.* (*Scolops*) *viridis* Ball, 1902	USA, California	6	–	Kuznetsova et al., 2009
99. *S. sulcipes* (Say, 1825)	USA, Illinois	6	–	Kuznetsova et al., 2009
Orgeriinae				
Ranissini				
100. *Elysiaca* (*Elysiaca*) *chomutovi* (Oshanin, 1879)	Kazakhstan	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
101. *E.* (*Eupolia*) *elliptica* (Oshanin, 1871)	Middle Asia	6	–	Kuznetsova, 1986
102. *E. oshanini* Emeljanov, 1972	Kazakhstan	6	–	Kuznetsova, 1986
103. *E. sclerosa* Emeljanov, 1972	Kazakhstan	6	–	Emeljanov & Kuznetsova, 1983
104. *Parorgerius platypus* (Fieber, 1866)	Greece	6	–	Kuznetsova, 1986
105. *Ranissus* (*Ranissus*) *edirneus* (Dlabola, 1957)	Greece	6	–	Kuznetsova et al., 2009
106. *Ranissus* (*Schizorgerius*) *scytha* (Oshanin, 1913)	Bulgaria	6	6	Kuznetsova et al., 2009
107. *Ranissus* sp.	Greece	6	–	Kuznetsova, 1986
108. *Sphenocratus hastatus* Oshanin, 1913	Kazakhstan	6	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
Almanini				
109. *Almana longipes* (Dufour, 1849)	Spain	4	4	Kuznetsova et al., 2009
110. *Bursinia* (*Bursinia*) *genei* (Dufour, 1849)	Greece	4	4	Kuznetsova & Kirillova, 1990: as *Bursinia* sp.
111. *B.* cf. *genei* Dufour, 1849	Spain	4	4	Kuznetsova et al., 2009
112. *Haumavarga fedtschenkoi* (Oshanin, 1879)	Kazakhstan	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
113. *Kumlika* (*Ammothetus*) *desertorum* (Oshanin, 1913)	Turkmenistan	–	4	Kaplin, 1985
114. *Mesorgerius rysakovi* Kusnezov, 1933	Kazakhstan	4	–	Kuznetsova, 1986
115. *M. zaisanensis* Kusnezov, 1933	Kazakhstan	4	–	Emeljanov & Kuznetsova, 1983: as *Stephanorgerius zaisanensis* Kusnezov, 1933
116. *Nymphorgerius alboniger* Emeljanov, 1972	Middle Asia	4	–	Kuznetsova, 1986
117. *N.* (*Anorgeriopus*) *auricularis* (Emeljanov, 1972)	Middle Asia	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
118. *N.* (*A.*) *bucharicus* (Oshanin, 1913)	Middle Asia	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
119. *N.* (*A.*) *skobelevi* (Oshanin, 1879)	Kazakhstan	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
120. *N. dimorphus* (Oshanin, 1879)	Middle Asia	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
121. *N.* (*Nymphorgerius*) *ivanovi* Kusnezov, 1928	Middle Asia	4	–	Kuznetsova, 1986
122. *N.* (*N.*) *medius* (Oshanin, 1879)	Middle Asia	4	–	Kuznetsova, 1986
123. *N.* (*Sphenocratoides*) *longiceps* Oshanin, 1879	Middle Asia	4	–	Kuznetsova, 1986
124. *Orgamarella lata* Emeljanov, 1969	Kazakhstan	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
125. *Ototettix jaxartensis* Oshanin, 1913	Middle Asia	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
126. *Repetekia orbicularis* Oshanin, 1913	Middle Asia Turkmenistan	4 –	– 4	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986; Kaplin, 1985
127. *Scirtophaca junatovi* (Emeljanov, 1972)	Kazakhstan	4	–	Emeljanov & Kuznetsova, 1983
128. *S.* (*Scirtophaca*) *tianshanskyi* (Oshanin, 1913)	Kyrgyzstan	4	–	Emeljanov & Kuznetsova, 1983; Kuznetsova, 1986
129. *Tigrahauda ototettigoides* (Oshanin, 1913)	Middle Asia	4	–	Kuznetsova, 1986
130. *T. tiarata* Oshanin, 1908	Kazakhstan	4	–	Kuznetsova, 1986
Orgeriini				
131. *Deserta bipunctata* (Ball, 1909)	USA, California	6	6	Kuznetsova et al., 2009
132. *Orgerius* (*Opsigonus*) *ventosus* Ball & Hartzell, 1922	USA, California	6	–	Kuznetsova et al., 2009
133. *O.* (*Orgerius*) *rhyparus* Stål, 1859	USA, California	6	6	Kuznetsova et al., 2009
8. FLATIDAE				
Flatinae				
Poekilopterini				
134. *Poekiloptera* sp. 1	Brazil	12	–	Kuznetsova et al., 1998
135. *Poekiloptera* sp. 2	Brazil	17	–	Kuznetsova et al., 1998
Flatini				
136. *Ormenis antoniae* Melichar, 1902	Brazil	10/8*	–	Kuznetsova et al., 1998
137. *Ormenis* sp.	Brazil	10/12*	–	Kuznetsova et al., 1998
138. *Phantia christophii* (De Rusiecka, 1902)	Uzbekistan	6	–	Kuznetsova & Kirillova, 1990
139. *Ph. subquadrata* (Herrich-Schäffer, 1838)	Bulgaria	6	–	New data

140. *Phylliana serva* (Walker, 1851)	Taiwan	–	12	Kuznetsova et al., 1998
141. *Salurnis marginella* (Guérin-Méneville, 1829)	China	6	–	Lin et al., 2011
9. FULGORIDAE				
Aphaeninae				
Aphaenini				
142. *Lycorma delicatula* (White, 1845)	USA, Pennsylvania China China	6 – 6	12 14 –	Lieu, 1934; Liu & Qin, 2020; Lin et al., 2011
Limoisini				
143. *Limois emelianovi* Oshanin, 1908	Far East of Russia, Primorsky Krai	6	–	Kuznetsova, 1986
Dichopterinae				
Dorysarthrini				
144. *Dorysarthrus sumakowi* Oshanin, 1908	Turkmenistan	–	5	Kaplin, 1985
Fulgorinae				
Laternariini				
145. *Pyrops candelaria* (Linnaeus, 1758)	China	6	10	Kershaw & Kirkaldy, 1910
Strongylodematinae				
Capocleini				
146. *Capocles podlipaevi* Emeljanov, 2007	South Africa	5/6*, 4/6*	–	Kuznetsova et al., 2009
10. ISSIDAE				
Hysteropterinae				
Hysteropterini				
147. *Agalmatium bilobum* (Fieber, 1877)	Kazakhstan Greece & Italy	11 11	8 8	Emeljanov & Kuznetsova, 1983; Maryańska-Nadachowska et al., 2006
148. *A. flavescens* (Olivier, 1791)	Spain	11	–	Maryańska-Nadachowska et al., 2006
149. *Apedalamus abruzicus* (Dlabola, 1983)	Italy	10	–	Kuznetsova et al., 2010: as *Mulsantereum abruzicum* (Dlabola, 1983)
150. *Bergevinium malagense* (Matsumura, 1910)	Spain	9	–	Maryańska-Nadachowska et al., 2006
151. *Brachyprosopa* (*Brachyprosopa) umnovi* Kusnezov, 1929	Turkmenistan	–	6–7	Kaplin, 1985
152. *Bubastia obsoleta* (Fieber, 1877)	Greece	10	–	Kuznetsova et al., 2010
153. *B. saskia* Dlabola, 1984	Greece	10	–	Kuznetsova et al., 2010
154. *B. taurica* (Kusnezov, 1926)	Russia	10	–	Maryańska-Nadachowska et al., 2006
155. *Falcidius doriae* (Ferrari, 1884)	Italy	10	–	Kuznetsova et al., 2010
156. *Hysteropterum albaceticum* Dlabola, 1983	Spain	10	–	Maryańska-Nadachowska et al., 2006
157. *H. vasconicum* Gnezdilov, 2003	Spain	10	–	Maryańska-Nadachowska et al., 2006
158. *Kervillea* (*Corymbius*) *tekirdagica* (Dlabola, 1982)	Greece	10	–	Kuznetsova et al., 2010
159. *K.* (*Kervillea*) *basiniger* (Dlabola, 1982)	Greece	10	–	Kuznetsova et al., 2010
160. *K.* (*K.*) *scoleogramma* (Fieber, 1877)	Turkey	12	–	New data
161. *Latilica maculipes* (Melichar, 1906)	Italy	10	–	Maryańska-Nadachowska et al., 2006
162. *Mycterodus* (*Mycterodus*) *etruscus* Dlabola, 1980	Italy	16	–	Kuznetsova et al., 2010
163. *M.* (*M.*) *intricatus* Stål, 1861	Crimea	20	–	Kuznetsova et al., 2010
164. *M.* (*Semirodus*) *colossicus* (Dlabola, 1987)	Greece	18	–	Kuznetsova et al., 2010
165. *M.* (*S.*) *pallens* (Stål, 1861)	Greece	18	9	Maryańska-Nadachowska et al., 2006
166. *Palaeolithium distinguendum* (Kirschbaum, 1868)	Spain	7–13	8	Maryańska-Nadachowska et al., 2006
167. *Palmallorcus balearicus* (Dlabola, 1982)	Spain	9–11	–	Maryańska-Nadachowska et al., 2006
168. *P. nevadensis* (Linnavuori, 1957)	Spain	10	–	Maryańska-Nadachowska et al., 2006
169. *P. punctulatus* (Rambur, 1840)	Spain	4?	–	Maryańska-Nadachowska et al., 2006
170. *Scorlupaster asiaticum* (Lethierry, 1878)	Kazakhstan	9	–	Kuznetsova et al., 2010
171. *Scorlupella discolor* (Germar, 1821)	Crimea	6	–	Kuznetsova et al., 2010
172. *Tingissus guadarramense* (Melichar, 1906)	Spain	10	6	Maryańska-Nadachowska et al., 2006: as *T. tangirus* (Matsumura, 1910)
173. *Tshurtshurnella pythia* Dlabola, 1979	Greece	12	7	Maryańska-Nadachowska et al., 2006
174. *Zopherisca penelopae* (Dlabola, 1974)	Greece	24	–	Maryańska-Nadachowska et al., 2006
175. *Z. skaloula* (Gnezdilov & Drosopoulos, 2006)	Greece	30	–	Maryańska-Nadachowska et al., 2006: as *Z. tendinosa* (Spinola, 1839)
176. *Z. tendinosa tendinosa* (Spinola, 1839)	Greece	28	–	Kuznetsova et al., 2010
Issinae				
Issini				
177. *Issus coleoptratus* (Fabricius, 1781)	Ukraine Spain France	20 13 20	– – –	Ivanov, 1928; Maryańska-Nadachowska et al., 2006; Dufour, 1833
178. *I. lauri* Ahrens, 1814	Italy	13	13, 13/12*	Maryańska-Nadachowska et al., 2006
179. *Latissus dilatatus* (Fourcroy, 1785)	Italy	12	–	Kuznetsova et al., 2010
11. KINNARIDAE				
Kinnarinae				
Oeclidiini				
180. *Oeclidius* pr. *nanus* Van Duzze, 1914	USA, California	6	–	Kuznetsova & Maryańska-Nadachowska, 2006
12. LOPHOPIDAE				
Lophopinae				
Lophopini				
181. *Pyrilla perpusilla* (Walker, 1851)	India	6	28	Quadri & Aziz, 1950
Menoscinae				
Elasmoscelini				
182. *Elasmoscelis trimaculata* Walker, 1851	Ethiopia	6	–	Kirillova, 1993: as *E. bimacula* Melichar, 1915
13. MEENOPLIDAE				
Kermesiinae				
Kermesiini				
183. *Nisia carolinensis* Fennach, 1971	Taiwan	6	–	Kuznetsova et al., 1998

14. NOGODINIDAE				
Bladininae				
Bladinini				
184. *Bladina mimica cymula* Kramer, 1976	Unknown	9	–	Kuznetsova et al., 1998
Nogodininae				
Nogodinini				
185. *Biolleyana pictifrons* (Stål, 1864)	Brazil	24	–	Kuznetsova et al., 1998
Pisachini				
186. *Pisacha* sp.	Vietnam	24	–	Kuznetsova et al., 1998
15. RICANIIDAE				
Ricaniinae				
187. *Orosanga japonica* (Melichar, 1898)	Georgia	10–12	–	Kuznetsova & Kirillova, 1990
188. *Ricania speculum* (Walker, 1851)	China	12	–	Lin et al., 2011
16. TETTIGOMETRIDAE				
Nototettigometrinae				
189. *Nototettigometra* (*Nototettigometra*) *patruelis* (Stål,1855)	Ethiopia	3	–	Kirillova, 1993: as *Hilda patruelis* (Stål, 1855)
Tettigometrinae				
190. *Tettigometra* (*Mitricephalus*) *eremi* Lindberg, 1948	Kyrgyzstan	6	11/12*	Kuznetsova & Kirillova, 1990
191. *T.* (*M.*) *macrocephala* Fieber, 1865	Uknown	6	–	New data
192. *T.* (*M.*) *obliqua* Panzer, 1799	Ukraine Kyrgyzstan	6 6	12 –	Ivanov, 1928; Kuznetsova & Kirillova, 1990
193. *T.* (*Stirometra*) *costulata* Fieber, 1865	Uzbekistan	5, 5/6*	6	Kuznetsova & Kirillova, 1990
194. *T.* (*Tettigometra*) *varia* Fieber, 1865	Kazakhstan	6	7	Kuznetsova & Kirillova, 1990
195. *T.* (*T.*) *vitellina* Fieber, 1865	Tajikistan & Kyrgyzstan	6	6–15	Kuznetsova & Kirillova, 1990
196. *T. atra* Hagenbach, 1825	Ukraine	6	12	Ivanov, 1928
17. TROPIDUCHIDAE				
Tropiduchinae				
Tambiniini				
197. *Kallitaxila sinica* (Walker, 1851)	Taiwan	6	–	Kuznetsova et al., 1998
198. *Tambinia bizonata* Matsumura, 1914	Taiwan	6	–	Kuznetsova et al., 1998
Cyphoceratopini				
199. *Achilorma bicincta* (Spinola, 1839)	Brazil	6	–	Kuznetsova et al., 1998
200. *Numicia viridis* Muir, 1931	South Africa	4	8	Bayer, 1965

* Various numbers of follicles/ovarioles in different testes/ovaries of the same specimen.