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# Karyotypes, Sex-Chromosome Systems, and Testis Structure in Fulgoroidea (Auchenorrhyncha, Homoptera, Insecta)

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Karyotypes (number and size of chromosomes, sex -determining system) and testis structure (number of testicular follicles) of 37 species belonging to 24 genera of the little studied fulgoroid families Cixiidae, Meenoplidae, Derbidae, Achilidae, Nogodinidae, Tropiduchidae and Flatidae are presented. For Meenoplidae, Nogodinidae and Tropiduchidae data on the testis structure have been obtained for the first time. The data available for Fulgoroidea as a whole are reviewed.

Key words: karyotype, reproductive system, Auchenorrhyncha, Insecta, Homoptera.

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According to KUZNETSOVA (1993), karyotypes of 575 species belonging to 340 genera, 26 families and all four superfamilies of Auchenorrhyncha had been studied by the early 1990s. Since then approximately 35 more species have been karyotyped (DEY 1991; KIRILLOVA 1993; TIAN & YUAN 1997). The species studied altogether represent approximately 1.9 % of the world fauna of these insects. About one third of the species karyotyped belong to Fulgoroidea (see reviews: KIRILLOVA 1986; EMELYANOV & KIRILLOVA 1991; additional data: BARRION & SAXENA 1985; DEN BIEMAN 1988; KUZNETSOVA 1992; KIRILLOVA 1993). It should be noted however that the majority of these data concern the families Delphacidae and Dictyopharidae studied fairly completely (KIRILLOVA 1991; KUZNETSOVA 1985). For other families of Fulgoroidea (altogether 17 families, according to EMELYANOV 1987) data are either lacking (Achilixiidae and Kinnaridae) or fragmentary: in Flatidae 10 species of 9 genera have been studied; for 12 other families data are available from one species in Nogodinidae to two to five species in Cixiidae, Derbidae, Fulgoridae, Lophopidae.

In relation to the structure of testes not more than 140 species of Auchenorrhyncha (approximately 0.4% of the known species) have been studied. Of these two thirds belong to Fulgoroidea (see review: EMELYANOV & KUZNETSOVA 1983; additional data: KUZNETSOVA 1985, 1992; KIRILLOVA 1989, 1993; KUZNETSOVA & KIRILLOVA 1990). As in the case of karyotypes, the most numerous data are available for the families Delphacidae and Dictyopharidae (KIRILLOVA 1989; KUZNETSOVA 1985). Of 15 other families Kinnaridae, Meenoplidae, Achilixiidae, Nogodinidae, Tropiduchidae and Eurybrachidae remain completely uninvestigated. In other families from one (Derbidae, Lophopidae, Ricaniidae, Flatidae) to six (Tettigometridae, Cixiidae, Fulgoridae) species have been studied.

The taxonomic and phylogenetic importance of the characters of the karyotype (its structure, number of chromosomes, chromosome system of sex determination) and arrangement of the reproductive system (number of testicular follicles and ovarioles, and shape of accessory glands) in Auchenorrhyncha was repeatedly shown with reference to different groups, including Fulgoroidea (IVANOV 1926, 1928; HALKKA 1959: EMELYANOV & KUZNETSOVA 1983; KAPLIN 1985; KUZNETSOVA 1985, 1992; EMELYANOV & KIRILLOVA 1989, 1991; KIRILLOVA 1989, 1991, BEDNARCZYK 1993).

In the present work new data on the karyotypes and structure of testes (number of follicles) are represented for the little studied fulgoroid families Cixiidae, Meenoplidae, Derbidae, Achilidae, Nogodinidae, Tropiduchidae, and Flatidae. For Meenoplidae, Nogodinidae and Tropiduchidae data on the structure of testes have been obtained for the first time. The data available for Fulgoroidea as a whole are reviewed.

## Material and Methods

A total of 37 species belonging to 24 genera and 7 families of Fulgoroidea were studied (Table 1). For 16 species of 15 genera representing 6 families (except Meenoplidae) data both on karyotypes and number of testicular follicles were obtained. In other species only the number of follicles was determined.

Young males were fixed in an ethanol-acetic mixture (3:1). The gonads were extracted from the abdomen preliminarily stained with acetorcein. Testicular follicles were separated and squashed on a slide in a drop of 45% or 70% acetic acid depending on the duration of the material's preservation in fixative. The preparations were made permanent by a dry ice technique (CONGER & FAIRCHILD 1953). Further, the preparations were additionally stained with 2% Giemsa solution, air dried, and mounted in Euparal.

Permanent chromosome preparations of the species studied have been deposited in the Department of Karyosystematics of the Zoological Institute, RAS. Genitals of the males from which the preparations were made were also deposited and provided with corresponding numbers. This is particularly important for specimens which have not been identified to a species and also for new species for which data on the karyotype and number of testicular follicles may be used in future descriptions.

## Results and Discussion

All data on the karyotypes, and structure of tes tes, and in some cases also on the structure of ova ries (number of ovarioles), in representatives of th families Cixiidae, Meenoplidae, Derbidae, Achilida Nogodinidae, Tropiduchidae, and Flatidae, bot original and from the literature, are given in Table 1

### Family Cixiidae

New data were obtained for three species.

The only male *Cixius cunicularius* studied ha five follicles in each testis. The number of chromo somes, 2n = 30, 29 (28+XX/X0) in this species wa determined earlier (HALKKA 1959), but the photo graph of the karyotype is published by the presen authors for the first time (Figs 1 & 2). Haploid se (in MI, i.e. metaphase of the first division of meiosis includes 14 autosomal bivalents and a univalen X-chromosome (meioformula n = 14+X). Amon bivalents there are 4-5 relatively larger; th X-chromosome is one of the smallest elements in th set.

Cixiidae is regarded (ASCHE 1987; EMELYANO 1990) as one of the most primitive families of Fu goroidea. Chromosome data are available only fo Cixiinae of the three subfamilies accepted by EMEL YANOV (1989). This subfamily includes the ma jority of representatives of Cixiidae. In the fiv studied species belonging to three genera of th tribes Cixiini and Pentastirini, chromosome num bers vary from 2n = 19 to 2n = 31 (in males). should be noted that in both tribes the karyotype 2 = 30, 29 (28+XX/X0) was discovered, which wa earlier adopted as the initial one in the evolution o Fulgoroidea as a whole (KUZNETSOVA 1987; EMEL YANOV & KIRILLOVA 1991).

The number of testicular follicles in Cixiidae relatively variable and may differ even in clos species (*Cixius* spp.). In most species the numbe of follicles is 4 (4 species, 3 genera) or 6 (3 specie 3 genera) per testis in males, number 6 being re garded as the plesiomorphic state of the testis Fulgoroidea (EMELYANOV & KUZNETSOVA 198 KUZNETSOVA 1987). It is noteworthy that *Bothrio cera* sp. n. and *B. tenalis,* belonging to the sma (only two genera) and morphologically distin subfamily Bothriocerinae have 2 follicles per te tis, the latter being apparently the maximal degre of oligomerization of this character in Aucheno rhyncha. Testes of such structure were found, wi the exception of *Bothriocera* spp., only in *Form levu quadrimaculatus* from Derbidae (the prese paper) and earlier (BEDNARCZYK 1993) in *Zyginia viaduensis* from Cicadellidae (Cicadelloidea).

Table 1

Data available on karyotypes and number of testicular follicles for 7 families of Fulgoroidea

| Taxon | No. specimens examined | 2n (in male) | No. of follicles per testis | Locality | References |
|---|---|---|---|---|---|
| Cixiidae | | | | | |
| 1. *Bothriocera* sp. n. | | – | 2 | Panama | present data |
| 2. *B.tinealis* Burm. | 1 ♀ | – | 2 | Brasil | present data |
| Bothriocerinae | | | | | |
| Cixiinae | | | | | |
| Oecleini | | | | | |
| 3. *Mundopa kotoshonis* Mats. | 1 ♂ | – | 4 | Taiwan | present data |
| | 3 ♀♀ | – | 14* | | |
| Cixiini | | | | | |
| 4. *Cixius borusticus* Wagn. | 1 ♂ | – | 4 | Russia | KUZNETSOVA & KIRILLOVA 1990 |
| 5. *C. cuncularius* L. | 1 ♂ | 29(28+X) | | Finland | HALKKA 1959 |
| | 1 ♂ | 29(28+X) | 5 | Russia (St.Petersburg) | present data |
| 6. *C. pilifer* Melich. | | 25(24+X) | – | India | RAY-CHAUDHURI *et al.* 1967 |
| 7. *C. stigmaticus* Germ. | | – | 4 | Ukraine | IVANOV 1928 |
| Duilini | | | | | |
| 8. *Hemitropis* sp. | 6 ♂♂ | – | 4 | Kazakhstan | IVANOV 1928 |
| Pentastirini | | | | | |
| 9. *Melanoliarus* sp. | 1 ♂ | – | 6 | Cuba | KUZNETSOVA & KIRILLOVA 1990 |
| 10. *Pentastiridius hodgarti* Dist. | – | 19(18+X) | – | India | BHATTACHARYA & MANNA 1973 (as *Oliarus*) |
| 11. *P. leporinus* L. | 2 ♂♂ | 31(30+X) | – | Finland | HALKKA 1959 (as *Oliarus*) |
| | – | – | 6 | Ukraine | IVANOV 1928 (as *Oliarius*) |
| 12. *Eumecurus abyssinicus* Van Stalle | 3 ♂♂ | 29(28+X) | 6 | Ethiopia | KIRILLOVA 1993 |
| Meenoplidae | | | | | |
| Kermesiinae | | | | | |
| 13. *Nisia carolinensis* Fennach | 1 ♂ | – | 6 | Taiwan (Taichung) | present data |
| 14. *N. nervosa* Motsch. | – | 27(26+X) | India | | PARIDA & DALUA 1979, 1981 (as *N. atrovenosa* Leth.) |
| Meenoplinae | | | | | |
| 15. *Meenoplus albosignatus* Fieb. | 4 ♀♀ | 27(26+X) | – | Armenia | KUZNETSOVA & KIRILLOVA 1990 |
| 16. *Meenoplus* sp. | – | 27(26+X) | – | India | PARIDA & DALUA 1981 |
| Derbidae | | | | | |
| Cedusinae | | | | | |
| Cedusini | | | | | |
| 17. *Cedusa* sp.n. | 1 ♂ | – | 5 | Brazil | present data |
| 18. *Cedusa* sp. | 4 ♂♂ | – | 5 | Mexico | present data |
| Derbinae | | | | | |
| Derbini | | | | | |
| 19. *Mysidia* sp. | 1 ♂ | 27(26+X) | 4 | Brazil | present data |
| Cenchreini | | | | | |
| 20. *Persis stali* Muir | 3 ♂♂ | 27(26+X) | 4 | Brazil | present data |
| 21. *Vekunta* sp.n. | 1 ♂ | – | 6 | Vietnam | present data |
| 22. *Omolicna cubana* Fenn. | 2 ♂♂ | 27(26+X) | 4 | Cuba | KUZNETSOVA & KIRILLOVA 1990 |

Contd Table 1

| | | | | | |
|---|---|---|---|---|---|
| Otiocerinae | | | | | |
| Rhotanini | | | | | |
| 23. *Formalevu quadrimaculatus* (Muir) | 2 ♂♂ | 27(26+X) | 2 | Taiwan | present data |
| Otiocerini | | | | | |
| 24. *Otiocerus wolfii* Kirby | – | 27(26+X) | – | USA | HALKKA & HEINONEN 1964 |
| Phenicini | | | | | |
| 25. *Phenice bicornis* Muir | – | 27(26+X) | – | Ghana | LESTON 1961 |
| Zoraidini | | | | | |
| 26. *Diostrombus carnosus* Westw. | – | 27(26+X) | | India | BHATTACHARYA & MANNA 1967, 1973 |
| 27. *D. politus* Uhler | 1 ♂ | – | 3 | Vietnam | present data |
| 28. *Proutista moesta* Westw. | – | 25(24+X) | | India | BHATTACHARYA & MANNA 1967 (as *Phenice*) |
| Achilidae | | | | | |
| Achilinae | | | | | |
| Myconites (supertribe) | | | | | |
| Plectoderini | | | | | |
| 29. *Amblycratus pallidus* Uhler | – | | 6 | | FENNAH 1950 |
| 30. *Amblysellus* sp. | 2 ♂♂ | – | 3 | Brazil | present data |
| 31. *Catonia* sp. | 1 ♂ | 27(26+X) | 3 | Brazil | present data |
| 32. *Catonia sanctae-luciae* (Fenn.) | – | | 6 | | FENNAH 1950 |
| 33. *Deferunda* sp. | 2 ♂♂ | – | 3 | Vietnam | present data |
| 34. *Juniperia indella* Ball | | – | 3 | USA | O'BRIEN 1971 |
| 35. *Momar maculifrons* Van Duzee | – | 27(26+X) | 5 | USA | O'BRIEN 1971 |
| 36. *Plectoderes* sp.1 | 1 ♂ | – | 4 | Brazil | present data |
| 37. *Plectoderes* sp.2 | 3 ♂♂ | – | 3 | Brazil | present data |
| 38. *Plectoderes* sp.3 | 1 ♂ | 27(26+X) | 6 | Brazil | present data |
| 39. *Synecdoche helenae* Van Duzee | – | 26(24+XY) | 7 | USA | O'BRIEN 1971 |
| Achilites (supertribe) | | | | | |
| Seviini | | | | | |
| 40. *Sevia* sp.n.1 | 1 ♂ | 27(26+X) | 6 | Brazil | present data |
| 41. *Sevia* sp.n.2 | 1 ♂ | 24(22+XY) | 6 | Brazil | present data |
| 42. *Achilidae* sp.1 | 1 ♂ | – | 3 | Vietnam | present data |
| 43. *Achilidae* sp.2 | 1 ♂ | – | 3 | Vietnam | present data |
| 44. *Achilidae* sp.3 | 1 ♂ | – | 3 | Vietnam | present data |
| 45. *Achilidae* sp.4 | 1 ♂ | – | 3 | Vietnam | present data |
| 46. *Achilidae* sp.5 | 1 ♂ | – | 3 | Vietnam | present data |
| 47. *Achilidae* sp.6 | 1 ♂ | – | 3 | Vietnam | present data |
| Nogodinidae | | | | | |
| Nogodininae | | | | | |
| Bladinini | | | | | |
| 48. *Bladina magnifrons* Walker | 1 ♂ | 27(26+X) | – | Panama | HALKKA 1961 |
| 49. *Bladina mimica cymula* Kramer | 1 ♂ | – | 9 | | present data |
| Nogodinini | | | | | |
| Nogodinina | | | | | |
| 50. *Biolleyana pictifrons* Stal | 1 ♂ | 27(26+X) | 24 | Brazil | present data |
| Varciini | | | | | |
| Sassulina | | | | | |
| 51. *Mindura subfasciata kotoshonis* Mats. | 3 ♂♂ | 26(24+XY) | 5 | Taiwan | present data |
| 52. *Pisacha* sp.n. | 1 ♂ | 26(24+XY) | 24 | Vietnam | present data |

Contd Table 1

| | | | | | |
|---|---|---|---|---|---|
| Tropiduchidae | | | | | |
| Tambiniini | | | | | |
| 53. *Kallitaxila sinica* (Walker) | 4 ♂♂ | – | 6 | Taiwan | present data |
| 54. *Tambinia bizonata* (Mats.) | 2 ♂♂ | 25(24+X) | 6 | Taiwan | present data |
| Catullini | | | | | |
| 55. *Barunoides albosignata* Dist. | – | 25(24+X) | – | India | BHATTACHARYA & MANNA 1973 |
| Cyphoceratopini | | | | | |
| 56. *Achilorma* ? *bicincta* Spinola | 2 ♂♂ | 27(26+X) | 6 | Brazil | present data |
| Tropiduchini | | | | | |
| 57. *Varma distanti* Melich. | 2 ♂♂ | 29(28+X) | – | India | BHATTACHARYA & MANNA 1973 |
| Flatidae | | | | | |
| Flatinae | | | | | |
| Poekilopterini | | | | | |
| 58. *Poekiloptera* sp.1 | 1 ♂ | 23(22+X) | 12 | Brazil | present data |
| 59. *Poekiloptera* sp.2 | 1 ♂ | 23(22+X) | 17 | Brazil | present data |
| *Poekiloptera* male | 1 ♂ | 23(22+X) | 17/15** | Brazil | present data |
| 60. *P. phalaenoides* L. | – | 22(20+XY) | – | Panama | HALKKA 1961 |
| Seliziini | | | | | |
| 61. *Paraketumala* spp. | – | 27(26+X) | – | India | BHATTACHARYA & MANNA 1973 |
| 62. *Paraketumala* sp. | – | 26(?) | – | India | PARIDA & DALUA 1981 |
| Nephesini | | | | | |
| 63. *Anormenis septentrionalis* Spin. | – | 27(26+X) | | USA | BORING 1907 (as *Poekiloptera*)<br>HALKKA 1959 (as *Ormenis*) |
| 64. *Geisha distinctissima* Walker | – | 23(22+X) | | Japan | KUROKAWA 1953 |
| 65. *Melicharia sinhalana* Kirk. | – | 25(24+X) | | India | BHATTACHARYA & MANNA 1967;<br>BHATTACHARYA 1973<br>(as *M. quadrata* Kirby) |
| 66. *Metcalfa pruinosa* Say | – | 27(26+X) | | USA | BORING 1907 (as *Poekiloptera*);<br>HALKKA 1959 (as *Ormenis*) |
| Flatini | | | | | |
| 67. *Siphanta* sp. | | 27(26+X) | – | Australia | WHITTEN 1965 |
| 68. *Ormenis* sp. | – | 24(22+XY) | 10/12** | Brazil | present data |
| | 1 ♂ | 24(22+XX) | – | | |
| | 1 ♀ | | | | |
| 69. *O. antoniae* | 1 ♂ | – | 10/8** | Brazil | present data |
| 70. *Phylliana serva* Walker | 3 ♀♀ | – | 12* | Taiwan | present data |
| 71. *Phantia christofii* de Rusiecka | 2 ♂♂ | 28(26+XY) | 6 | Uzbekistan | KUZNETSOVA & KIRILLOVA 1990 |
| Flatoidinae | 1 ♂ | | | | |
| 72. *Flatoidinus* sp. | | ? 28 | – | Panama | HALKKA 1961 |

*Number of ovarioles per ovary in females.

**Dissimilar number in different testes of male.

The species *Mundopa kotoshonis* was represented in the authors' material not only by males but also by females, in which ovaries were examined. Data on the structure of ovaries in Auchenorrhyncha are even more scanty than on testes (see EMELYANOV & KUZNETSOVA 1983; KAPLIN 1985). In Cixiidae such data were earlier available for *Cixius stigmaticus* (13-18 ovarioles per ovary) and *Pentastiridius leporinus* (20-30) (IVANOV 1928; the number of ovarioles was determined by the author approximately) and also for *Cubana* spp. (28) and *Cubanella* spp. (15-17) (FENNAH 1948). In females of *M. kotoshonis* each ovary was shown to contain 14 ovarioles (without polymorphism), which does not reach beyond the limits of variation of this character known for cixiids.

New data concern the structure of testes in *Nisia carolinensis* and were obtained for the first time for the family as a whole.

*N. carolinensis* belonging to the primitive subfamily Kermesiinae has 6 follicles per testis in males. The scanty data available on the karyotypes of Meenoplidae have already been discussed (EMELYANOV & KIRILLOVA 1991); no new data have been published since then. The family is divided into the subfamilies Kermesiinae and Meenoplinae (MUIR 1930). In both subfamilies in the studied 3 species of the genera *Nisia* and *Meenoplus* karyotype 2n = 28, 27 (26+XX/X0) has been found. It should be noted that this chromosome number is regarded (EMELYANOV & KIRILLOVA, 1991) as one of the most characteristic for all Fulgoroidea, more advanced than in Delphacidae or Cixiidae.

## Family Derbidae

New data were obtained for seven species.

*Mysidia* sp., *Persis* sp., and *Formolevu quadrimaculatus* belonging to three different tribes and two subfamilies (Derbinae, Otiocerinae) have 2n = 28, 27, XX/X0. At spermatogonial MI of all three species there are 13 autosomal bivalents and univalent X-chromosome (meioformula n = 13+X) (Figs 3, 4 & 7). At MII (metaphase of the second division) in a male *Persis* sp. the chromosome number is equal accordingly to 14 (13+X) and 13 (only autosomes) because the sex chromosome moved to one of the daughter nuclei (Figs 5 & 6). The karyotypes are similar in structure: each of them contains a very large bivalent 1, which exceeds in size almost two-fold the bivalent 2 following it in the gradually diminishing size row. It is interesting that at MI of *Mysidia* sp. and *F. quadrimaculatus* the X-chromosome has an unusually elongated form (Figs 3 & 7). Unfortunately, it was not possible to make a reliable identification of the sex chromosome in *Persis* sp.

Derbidae is one of the largest fulgoroid families and is mostly tropical. EMELYANOV (1994) divides this family into three subfamilies. For the relatively more advanced Derbinae and Otiocerinae a few data are available, both on karyotypes and testes, whereas for the primitive Cedusinae only data on the number of testicular follicles were obtained for *Cedusa* sp. from Mexico and *Cedusa* sp. n. from Brazil.

The first two subfamilies appear to be rather homogeneous karyologically: seven of the eight studied species representing six of the fourteen tribes have 2n = 28, 27 (26+XX/X0). The deviating karyotype 2n = 26, 25(24+XX/X0) was found in *Proutista moesta* from the higher tribe Zoraidini.

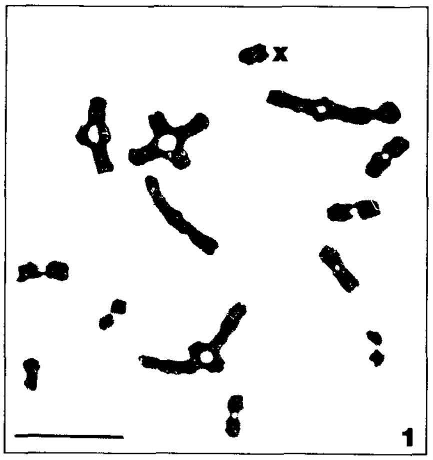
The structure of testes in derbids appeared to be more variable than the karyotypes: there are all numbers from 2 to 6. Both the studied species of *Cedusa* showed 5 follicles per testis. In Derbinae 4 follicles are predominant (3 species, 3 genera), however males of *Vekunta* sp. n. have 6 follicles per testis – supposedly an initial testis structure in Fulgoroidea (EMELYANOV & KUZNETSOVA 1983). In Otiocerinae two species have been studied: *Diostrombus politus* (Zoraidini) with 3 follicles per testis and *Formolevu quadrimaculatus* (Rhotanini) with 2 follicles per testis. The tribe Zoraidini displays the highest degree of specialization in the family (EMELYANOV 1994). Therefore it may be assumed that this is also indicated by an oligomerized number of follicles in *D. politus*. It is more difficult to explain why an ordinary representative of the most primitive tribe Rhotanini is characterized by the most deviating number of follicles. It has already been noted above that in Auchenorrhyncha testes consisting of 2 follicles present an example of maximal oligomerization and occur very seldom. However, it should be borne in mind that the tribe Rhotanini is characterized also by a number of morphological features differing it from other groups of Derbidae (EMELYANOV 1994).

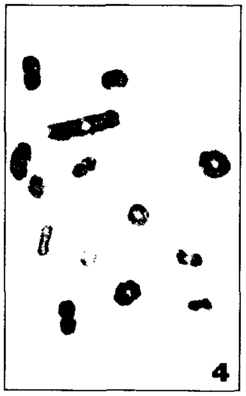
The Derbidae studied so far have never revealed a karyotype 2n = 30, 29 (28+XX/X), but very few species have been examined. Data available permit the assumption that the nearest ancestor of Derbidae had 2n = 28, 27 (26+XX/X0), which is also indicated by the above-mentioned structural similarity of such karyotypes in different subfamilies. This ancestor, it may be assumed, had 6 follicles per testis as *Vekunta* sp. n.

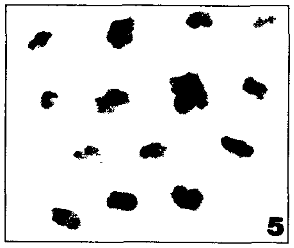
## Family Achilidae

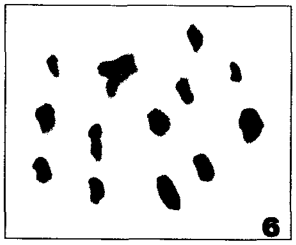
New data were obtained for 12 species.

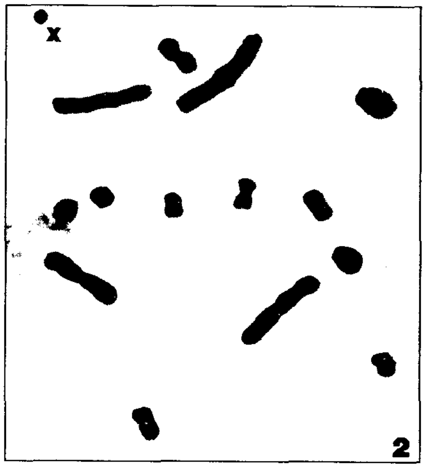
*Catonia* sp. and *Plectoderes* sp. 3 from the tribe Plectoderini differ from each other in the number of testicular follicles (accordingly 3 and 6 per testis) but have karyotypes coinciding in the number of chromosomes and sex-determining mechanism 2n = 28, 27 (26+XX/X0). At spermatogonial MI of

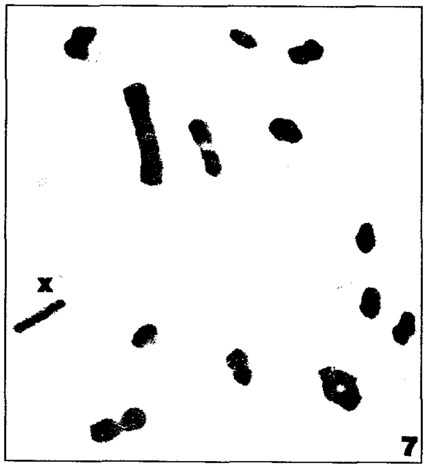


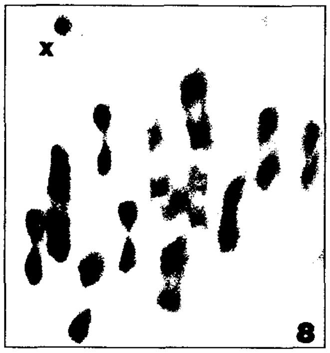


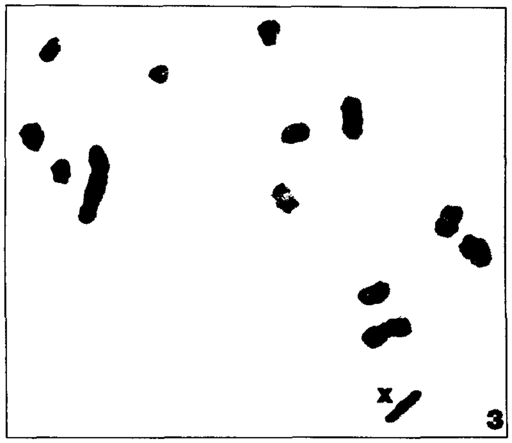


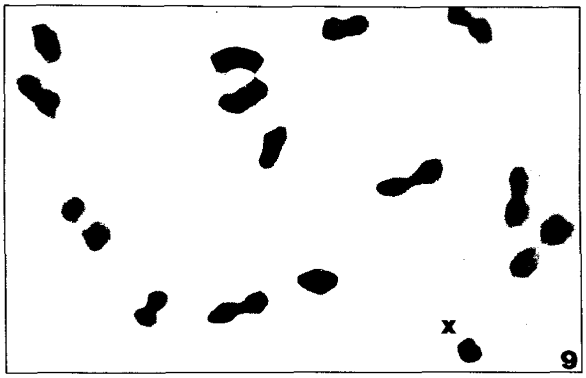












Figs 1 & 2. *Cixius cunicularius*. Two metaphases I. Fig. 3. *Mysidia* sp. Metaphase I. Figs 4-6. *Persis* sp. Fig. 4. Metaphase I. Fig. 5 & 6. Two daughter nuclei at metaphase II, one with X second without it. Fig. 7. *Formalevu quadrimaculatus*. Metaphase I. Fig. 8. *Catonia* sp. Metaphase I. Fig. 9. *Plectoderius* sp. Metaphase I. Bar equals 10 μm.

both species there are 13 autosomal bivalents and univalent X-chromosome (meioformula n = 13+X) (Figs 8 & 9). The karyotypes are similar in structure. Bivalents, except for the largest one, comprise a gradually diminishing size row; the X-chromosome is one of the smallest elements. At MI, the X-chromosome is always situated separately from the autosomes, this apparently being a typical feature of Auchenorrhyncha as a whole (KUZNETSOVA 1985).

Two males of *Sevia* available in the described material have 6 follicles per testis, but different karyotypes. Therefore they are regarded as different species.

*Sevia* sp. n. 1

2n = 28, 27 (26 + XX/X0)

At MI, similar to *Catonia* sp. and *Plectoderes* sp., there are 13 autosomal bivalents (meioformula n = 13+X); bivalents 2-13 gradually decrease in size and bivalent 1 is notably larger. The X-chromosome is situated on the periphery of the metaphase plate, always far from autosomes (Figs 10 & 11).

*Sevia* sp. n. 2

2n = 24, 24 (22+XX/XY)

At MI there are 11 autosomal bivalents and a large heteromorphic pair consisiting of X and Y chromosomes that form a pseudobivalent (meioformula n = 11+XY; Fig. 12). As in *Sevia* sp. n. 1 one pair of autosomes is very large, notably larger than bivalent 2. At AI (anaphase of the first division) the X and Y move to different poles (Fig. 13). As a result, in daughter nuclei at stage MII the same chromosome number is observed: n = 11+X and n = 11+Y (Figs14 & 15).

The available data (HALKKA 1959; KUZNETSOVA 1985; EMELYANOV & KIRILLOVA 1989, 1991) show that in Auchenorrhyncha the XY system is secondary in relation to X0, which predominates. In the majority of cases the XY system results from fusion of the X-chromosome and a homologue of one of the autosomal pairs in the initial karyotype with a greater number of autosomes (by one pair) and an X0 system. The newly arisen X and Y chromosomes are, as a rule, characterized by large size. This is particularly apparent in the neo-X chromosome, which, apart from the initial X-chromosome, includes also the "autosomal" part. Therefore species, ancestral for *Sevia* sp. n. 2 should have 2n = 26, 25 (24+XX/X0), i.e. by one pair of autosomes less than in *Sevia* sp. n.1.

Out of eight achilid species studied in the present work as regards testis structure seven have 3 or 6 follicles per testis (four and three species accordingly) and one species has 4 follicles. Species of the genus *Plectoderes* differ from each other in the number of follicles.

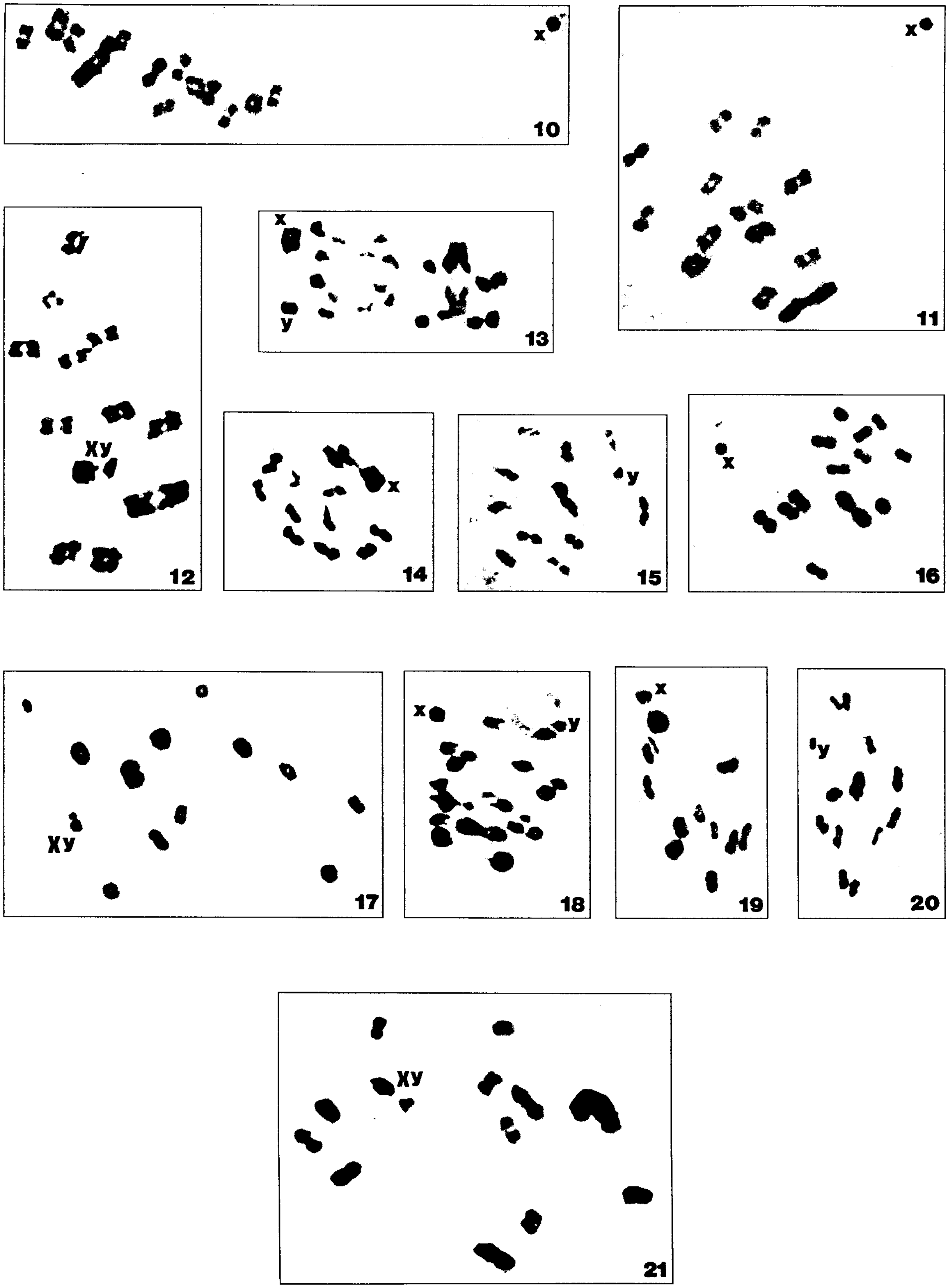
Achilidae is divided into 3 subfamilies (EMELYANOV 1991). Data on the structure of the testes and karyotypes are available only for Achilinae and only for Myconites and Achilites of 12 accepted tribes. As in Derbidae, karyotype 2n = 30, 29 (28+XX/X0) has not yet been found. Species with 2n = 28, 27 (26+XX/X0) and 6 or 3 follicles per testis are predominant. Karyotypes with the XX/XY-system (2n = 26, XX/XY in *Synecdoche helenae* and 2n = 24, XX/XY in S*evia* sp. n. 2) are secondary. Predominant in achilids are testes consisting of 3 follicles: apart from four species of four genera (see Table) such testes were discovered by the present authors in six species of Achilidae collected in Vietnam. Unfortunately, the species were identified only as to family. It would seem that the testes consisting of 6 follicles occurring in each of the two studied supertribes were ancestral in Achilinae. The ancestral karyotype of Achilinae apparently included 2n = 28, 27 (26+XX/X0). It is also possible to assume that these features were typical for the nearest ancestor of all Achilidae.

Family Nogodinidae

New data have been obtained for four species, the structure of testes being studied for the family for the first time.

In the only male *Biolleyana pictifrons* studied MI include 13 autosomal bivalents and a univalent X-chromosome (meioformula 13+X) (Fig. 16). On this basis the formula of diploid karyotype in this species was determined as 2n = 28, 27 (26+XX/X0).

At spermatogonial MI of *Mindura subfasciata kotoshonis* and *Pisacha* sp. n. (subtribe Sassulina, tribe Varciini) 12 autosomal bivalents and a heteromorphic pseudobivalent XY were discovered (meioformula n = 12+XY; Figs 17 & 21). In *M. subfasciata kotoshonis* bivalents form a gradually diminishing size row; the pseudobivalent is relatively not large, the Y-chromosome is twice as short as the X. At AI all chromosomes including sex chromosomes, divide reductionally (Fig. 18),



Figs 10 & 11. *Sevia* sp. 1. Two metaphases I. Figs 12-15. *Sevia* sp. 2. Fig.12. Metaphase I. Fig. 13. Anaphase I. Figs 14 & 15. Two daughter nuclei at metaphase II. Fig. 16. *Biolleyana pictifrons*. Metaphase I. Figs 17-20. *Mindura subfasciata kotoshonis*. Fig. 17. Metaphase I. Fig. 18. Anaphase I. Figs 19 & 20. Two daughter nuclei at Metaphase II. Fig. 21. *Pisacha* sp. n. Metaphase I. Bar equals 10 μm.

therefore at all MII 13 chromosomes are observed n = 12+X or n = 12+Y (Figs 19 & 20). On these grounds we determined the formula of diploid karyotype in both species was determined as 2n = 26, 26 (24+XX/XY). This karyotype is an evolutionarily secondary one, this being indicated by the derived type of sex chromosomes. The initial karyotype should include 2n = 26+X0 in the male, as in *B. pictifrons*. Being similar in karyotype, the species are very different in the structure of testes, which in *M. subfasciata kotoshonis* consist of 5 follicles each whereas in *Pisacha* sp. n. of 24. It should be noted here that in *B. pictifrons*, which belongs to the tribe Nogodinini, the testes also consist of 24 follicles each. So far, this is the largest follicle number known in Fulgoroidea as a whole. Previously, 20 follicles per testis in *Issus coleoptratus* of the family Issidae close to Nogodinidae was the largest follicle number known in Auchenorrhyncha (DUFOUR 1833).

FENNAH (1987) divides the family Nogodinidae into the subfamily Nogodininae with seven tribes and the monotypic subfamily Gastriniinae. Evidence including the authors' present data and the earlier known karyotype of *Bladina magnifrons* (2n = 26+X0 after HALKKA 1961) are available only for the tribes Bladinini and Varciini of Nogodininae. The secondary mechanism XX/XY in *M. subfasciata kotoshonis* and *Pisacha* sp. n. of Varciini permits these species to be regarded as evolutionarily advanced. In the latter species this also is indicated by the highly polymerized number of testicular follicles. It is noteworthy that *B. pictifrons* of Nogodinini also having a highly polymerized number of follicles retained karyotype with the initial system XX/X0.

For Bladinini data are available on two species. It was shown that *Bladina magnifrons* has 2n = 28, 27 (26+XX/X0) and *Bladina mimica cymula* 9 follicles per testis in males. EMELYANOV (EMELYANOV & KIRILLOVA 1991) believes that the tribe Bladinini should be placed in Issidae and regarded as a primitive subfamily, ancestral for typical issids. Thus the present authors' data concerning Nogodinini and Varciini are the first evidence for Nogodinidae *sensu stricto*. It can be assumed that evolutionarily initial for this group was karyotype 2n = 28, 27 (26+XX/X0) found in *B. pictiforns*. The data available are insufficient for speculation as to the initial structure of testes in Nogodinidae. Interestingly species of both Nogodinini and Varciini are characterized by 24 follicles, which is 4 times greater than the number of follicles (6) attributed to the nearest ancestor of Fulgoroidea.

Family Tropiduchidae

New data were obtained for 3 species, the stru ture of testes being studied for the family for t first time.

Males of *Tambinia bizonata* from the tribe Ta biniini have 6 follicles per testis. At MI 12 autos mal bivalents and an univalent X-chromoso were discovered (meioformula n = 12+X). Ther fore the formula of the karyotype was determin as 2n = 26, 25 (24+XX/X0).

*Achilorma bicincta* (tribe Cyphoceratopini) h the same number of seminal follicles as *T. biz* *nata* (6 per testis), but it has a different karyoty 2n = 28, 27 (26+XX/X0). The karyotype was stu ied at spermatogonial MI and also in spermatog nia. At the mitotic metaphase 27 chromosom were observed (Fig. 22). At this stage size t structure of the karyotype is distinct. As a rule th structure is less distinct in meiotic metaphase b cause of separate bivalents, which have interstiti chiasmata, disguising their true sizes. In the kary type there is one pair of very large and two pairs very small autosomes; in the diminishing size ro the X-chromosome is placed between bivalents 1 and 12 (Fig. 23). At the diakinesis – MI stages 1 elements are observed (Fig. 24). Therefore t meioformula of this species was determined as n 14 (13+X) and the formula of the diploid kary type as 2n = 28, 27 (26+XX/X0).

The family is divided into 15 tribes (FENNA 1982). Chromosome data are available for Ta biniini, Catulliini, Cyphoceratopini, and Tropiduchi one species having been studied in each (Table 1 Three variants of karyotypes were found. Speci from the two first tribes have the karyotype 2n 26, 25 (24+XX/X0), which is apparently evol tionarily secondary. Two other karyotypes are interest: *Varma distanti* (Tropiduchini) has t karyotype 2n = 30, 29 (28+XX/X0), which earl was adopted as initial in Fulgoroidea as a who (KUZNETSOVA 1987; EMELYANOV & KIRILLOV 1991). *Achilorma bicincta* (Cyphoceratopini) h the karyotype 2n = 28, 27 (26+XX/X0), which pr viously was adopted as the basic one in advanc fulgoroid families (EMELYANOV & KIRILLO 1991). *A. bicincta* has one very large pair of aut somes, whose origin could have been related to t fusion of two pairs of smaller autosomes in the a cestral karyotype. In this case it should be assum that the latter was 2n = 30, 29 (28+XX/X0) as *V. distanti*. Assuming that *A. bicincta* inherited karyotype from the nearest ancestor of Tropiduchidae, we should accept that the karyotype 2n = 30, 29 (28+XX/X0) in *V. distanti* is derived. For the resolution of this issue additional data are needed. We more definite conclusions can be mode concerning the structure of testes in the tropiduchid ancestor, which apparently had 6 follicles per testis. Such testes were discovered in males of all three species studied in this respect (tribes Tambiniini and Cyphoceratopini).

### Family Flatidae

New data were obtained for 9 species.

Three males of *Poekiloptera* from authors' material showed similar karyotypes. At MI, 11 autosomal bivalents and an univalent X-chromosome were found (meioformula n = 11 + X). Therefore the formula of the karyotype of the species was determined as 2n = 24, 23 (22 + XX/X0). Bivalents 1 and 2 are notably larger than bivalent 3 in the diminishing size row (Figs 25-27), which is also manifest at AI (Fig. 28); the X-chromosome is of medium size; the studied males, however, differed from each other in the number of follicles. One male had 12 follicles per testis, the second had 17 per testis and the third was mosaic having 17 follicles in one testis and 15 follicles in the other. On the basis of the essential differences in the testis structure the authors regard the first two males as different species.

In Auchenorrhyncha variation in follicle number (mosaicism) occurs not so frequently and mainly in species with relatively high numbers (see EMELYANOV & KUZNETSOVA 1983). Mosaicism was discovered by the present authors also in the only studied male of *Ormenis antoniae* (10 and 8 follicles in different testes) and the only studied male of *Ormenis* sp. (10 and 12 follicles in different testes). At MI of the latter 11 autosomal bivalents and a heteromorphic XY pseudobivalent were discovered (Fig. 29). Therefore the meioformula of this karyotype was determined as n = 11+X/Y) and the formula of the diplod set 2n = 24, 24 (22+XX/XY). Among autosomal bivalents a very large one is distinct; the X chromosome is similar in size to autosomes of average length and more than twice exceeds the Y chromosome, which is one of the smallest elements in the set. At MII and TII (telophase of the second division) 12 chromosomes including 11 autosomes and accordingly the X or Y chromosome are observed (Figs 30-32). Fig. 33 shows mitotic metaphase in a female, while Fig. 34 shows the karyogram. One can clearly see that the largest pair of autosomes is more than twice as large as the pair next to it in the diminishing size row. Each of the largest autosomes has an achromatin gap, which is seen also in the strongly spiralized chromosomes at the late metaphase (Fig. 35). These autosomes are apparently nucleoli forming.

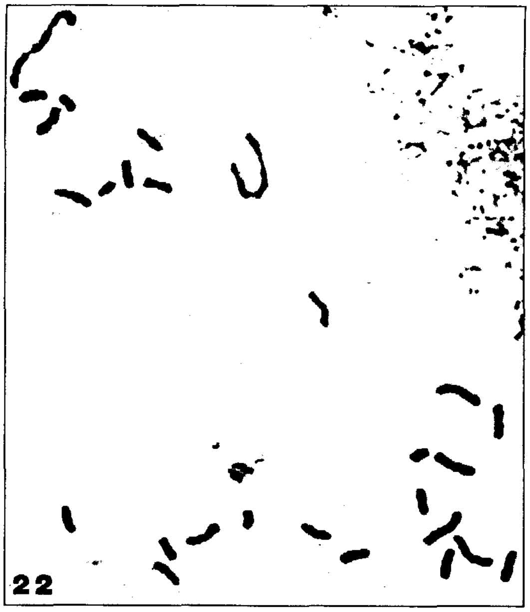
All three studied males of *Phylliana serva* showed 12 follicles per testis without mosaicism. Unfortunately we found only one MI in a single male was found. This metaphase plate included 13 elements, one of which was supposedly determined as a univalent X. Therefore meioformula was defined as n = 12+X, although without certainty.

Flatidae is one of the largest in families of Fulgoroidea. It is divided into the subfamily Flatinae with 8 tribes and the subfamily Flatoidinae (MUIR 1923, 1930; METCALF 1957). Altogether, karyotypes were studied in 13 species, including the present authors' new data of these, *Flatoidinus* sp. belongs to Flatoidinae, and others belong to Flatinae. Chromosome numbers vary from 2n = 22 to 2n = 28 in females. The majority of species were found to have the XX/X0 system, while three species showed XX/XY. The secondary origin of the XY system, which appeared as a result of X-autosome fusion (see above) is distinctly seen in the genus *Poekiloptera*. The number of autosomes in *P. phalaenoides* is one pair smaller (2n = 20+XY) than in related species with XO (2n = 22+XO). No species with 2n = 30, 29 (28+XX/X0) has been found in the family so far. The majority of species studied have 2n = 28, 27 (26+XX/XO), i.e. the karyotype which is considered (EMELYANOV & KIRILLOVA 1991) as the basic one in derived families of Fulgoroidea.

The testis structure has been studied in 5 species belonging to 4 genera of the tribes Poekilopterini and Flatini (Flatinae). Follicle numbers are mostly high (8/10 and higher), which differs flatids from other studied families, except probably Nogodinidae. Only the species *Phantia christofii* has 6 follicles per testis, i.e. the number regarded as evolutionarily initial for Fulgoroidea (EMELYANOV & KUZNETSOVA 1983).

## Conclusions

As a result of the authors' study in Cixiidae, Meenoplidae, Derbidae, Achilidae, Nogodinidae, Tropiduchidae and Flatidae the number of species with known karyotypes increased by one third and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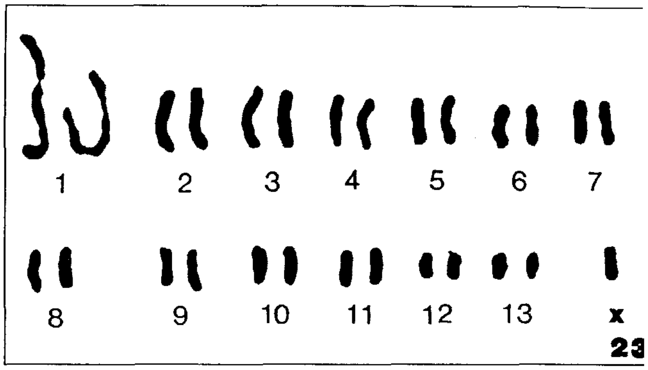

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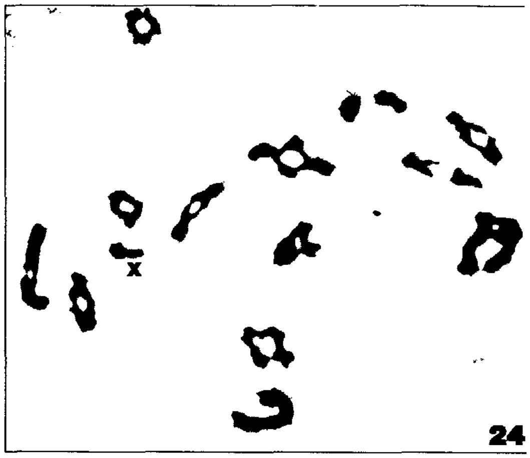

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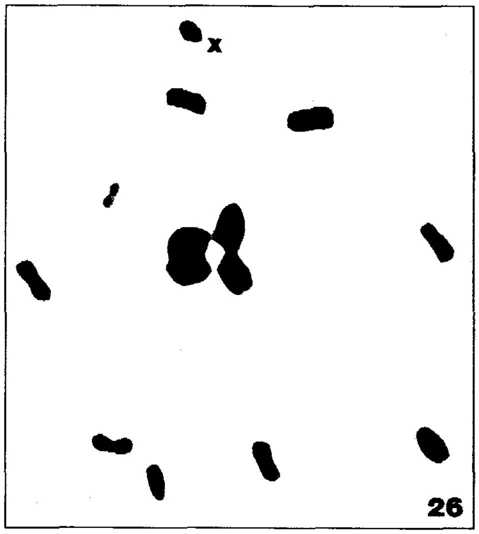

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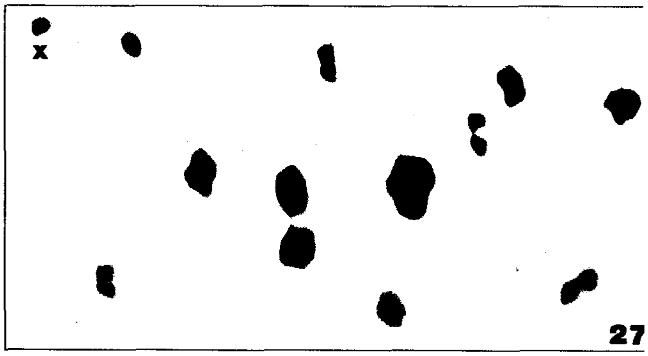

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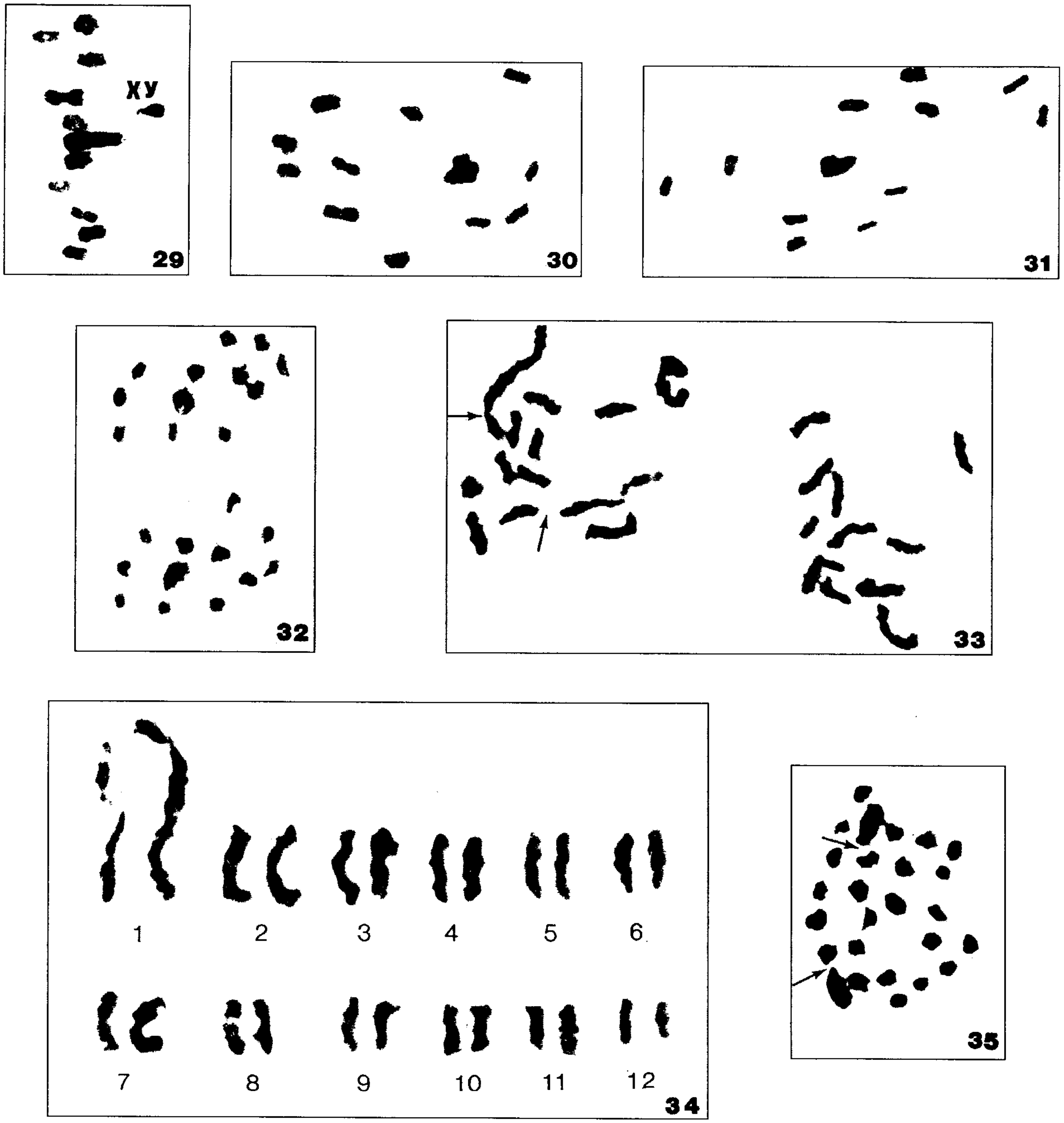
Figs 22-24. *Achilorma bicincta*. Fig. 22. Mitotic metaphase. Fig. 23. Karyogram of mitotic metaphase. Fig. 24. Metaphase I Figs 25-28. *Poekiloptera* sp. Fig. 25. Male 1. Metaphase I. Fig. 26. Male 2. Metaphase I. Fig. 27. Male 3. Metaphase I. Fig. 28 Male 3. Anaphase I. Bar equals 10 µm.



Figs 29-35. *Ormenis* sp. Fig. 29. Metaphase I. Figs. 30 & 31. Two daughter nuclei at metaphase II. Fig. 32. Telophase II. Fig. 33. Mitotic metaphase. Fig. 34. Karyogram of mitotic metahase. Arrows indicate breaks of chromosomes. Fig. 35. Late mitotic metaphase. Bar equals 10 µm.

attained 43. The number of studied genera also increased by one third and reached 37. In these families the number of species with known testis structure increased 4.5 times, attaining 47, while the number of studied genera reached 35. For Meenoplidae, Nogodinidae and Tropiduchidae data on testes were obtained for the first time.

In Fulgoroidea in total karyotypes of 181 species (approximately 2.4% of all known species) from 114 genera (approximately 6%) and 15 families

(Table 2) are known so far. The majority of species studied belong to Delphacidae (79 species, 46 genera) and Dictyopharidae (42 species, 21 genera). Fifty-two species and 47 genera fall to the remaining 13 families. Data for Achilixiidae and Kinnaridae are still lacking. The structure of testes has been studied up to the present in 139 species (approximately 2%) of 75 genera (approximately 4%) and 14 families of Fulgoroidea. Thirty-two species and 21 genera belong to Delphacidae and about 40 species and 19 genera to Dictyopharidae. Data for Kinnaridae, Achilixiidae, and Eurybrachidae are still lacking.

In Fulgoroidea chromosome numbers vary from 2n = 19 to 2n = 37 in males (Fig. 36). Karyotypes 2n = 30, 29 (28+XX/X0), 2n = 28, 27 (26+XX/X0), and 2n = 26, 26 (24+XX/XY) are statistically predominant. These karyotypes were found accordingly in 39%, 27% and 15% of the studied species. It should be noted that predominance of the first karyotype is almost completely provided by the families Delphacidae and Dictyopharidae. Of 13 other families it is found only in Cixiidae (2 species, 2 genera), Tropiduchidae (1 species) and Lophopidae (2 species 2 genera). The karyotype 2n = 26 (24+XX/XY) is considered to be evolutionarily secondary (see above). This karyotype was found in 8 families. As a rule it occurs in single species, their nearest relatives having the X0-system and by one pair more autosomes, i.e. 2n = 28, 27 (26+XX/X0). The latter karyotype is spread among fulgoroids most widely: it is found in all families, except Tettigometridae and Cixiidae.

The statistically predominant karyotype 2n = 30, 29 (28+XX/X0) was accepted as evolutionarily initial for Delphacidae (KIRILLOVA 1991) and Dictyopharidae (KUZNETSOVA 1985) and also for Fulgoroidea as a whole (KUZNETSOVA 1987; EMELYANOV & KIRILLOVA 1991). With regard to Delphacidae one argument was the predominance o this karyotype, which was found in 70% of studie species. Another argument was its occurrence i all the studied representatives of the primitive subfamilies Asiracinae, Kelisiinae and Stenocraninae The initial karyotype of Dictyopharidae was determined by means of superimposing data on the phylogenetic scheme (EMELYANOV 1980) of th advanced subfamily Orgeriinae with a subsequen extrapolation on the family. Arguments for Fulgoroidea as a whole were based exceptionally o data for these two families, particularly for Delphacidae regarded as one of the primitive fulgoroid families (ASCHE 1987; EMELYANOV 1987).

EMELYANOV & KIRILLOVA (1989, 1991) analysed the available data on karyotypes and conjectured that in Fulgoroidea the tendency to fusion o chromosomes was predominant and at later stage of evolution the karyotype 2n = 28, 27 (26+XX/X0 was fixed. The ancestral character of this karyotype for advanced fulgoroid families is confirme by the present authours' new data.

However, it would seem necessary to reconside the ancestral karyotype of Fulgoroidea as a whole It appears now that there are no grounds for acceptting the karyotype 2n = 30, 29, (28+XX/X0) a ancestral. The authours are inclined to believe tha the nearest ancestor of Fulgoroidea had 2n = 28, 27 (26+XX/X0). The argument is that this karyotype is most widely spread over recent Fulgoroidea. I was found in nearly every family studied. The hy-

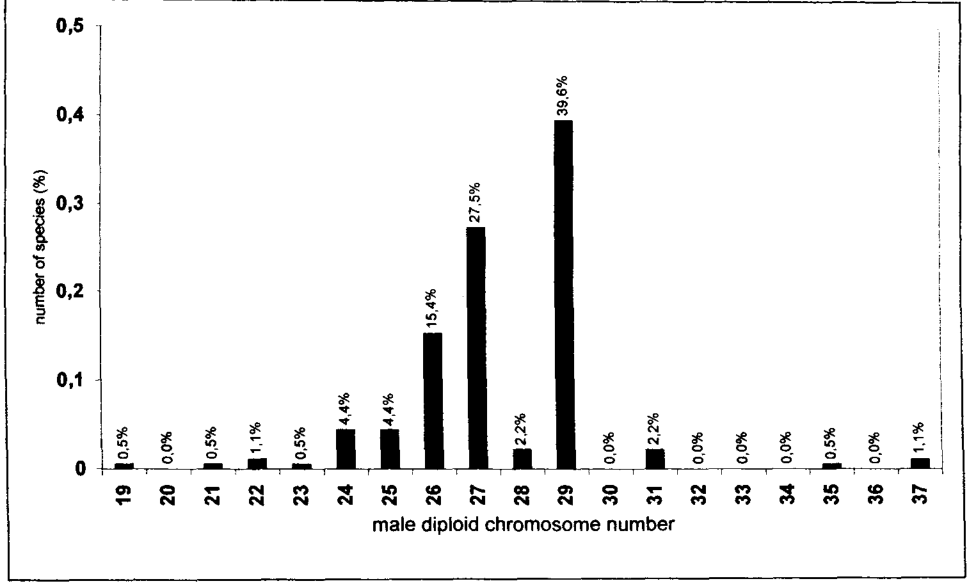


Fig. 36. Histogram showing the frequency distributions of male diploid chromosome numbers in Fulgoroidea.

pothesis is based on "...the first and central presumption in phylogenetic analysis", "...which claims: any similarity should be considered as inherited unless and until the reverse is reasonably proved" (RASNITSYN 1996).

One may object that the presented hypothesis contradicts the "biogenetic presumption" by RASTNITSYN (1996) because the presumed ancestral karyotype was not found in the most primitive fulgoroid families Tettigometridae and Cixiidae. However, very few species in these families have been studied. Moreover, some authors (BOURGOIN & CAMPBELL 1996) do not regard Tettigometridae as a primitive family. It should be noted that this standpoint is supported also by the available chromosome data. All the studied tettigometrids, including 4 species of the genus Tettigometra and *Hilda paruelis* Stal., showed the derived neo-XX/XY system of sex determination (KUZNETSOVA & KIRILLOVA 1990; KIRILLOVA 1993). The karyotype has been established reliably as 2n = 26, 26 (24+neo XX/XY) for *T. eremi* and *T. obliqua* and as 2n = 22, 22 (20+neo XX/XY) for *H. patruelis*. The karyotype 2n = 26, 26 (24+neo XX/XY) can easel be "deduced"from the putative ancestral 2n = 28, 27 (26+XX/X0) assuming one X-autosomal fusion in the latter. As has been noted above, these two karyotypes relatively frequently accompany each other in close species of many fulgoroid families. This fact confirms, although indirectly, that evolution of the karyotype of Fulgoroidea as a whole began from the number 27 (in males, but 28 in females), but not from 29 (in males, but 30 in females) as was previously assumed. Eventually, the authors believe that now there is one more important argument supporting this hypothesis. Karyotype 2n = 28, 27 (26+XX/X0) recently been discovered for the first time in Asiracinae, the most primitive subfamily of Delphacidae (unpublished data).

In the karyotype evolution of Fulgoroidea there were autosomal fusions and fissions and also repeated X-autosomal translocations. The latter led to de novo acquisition of the XY system. This system was described in 38 species belonging to 7 out of 15 fulgoroid families for which data are available (Table 2). Fissions apparently involved autosomes but never sex chromosomes. Up to now multiple sex chromosomes have not been found in both Fulgoroidea and Auchenorrhyncha as a whole. In this feature Auchenorrhyncha differ from some other homopteran groups, such as Aphidoidea and Coccidoidea, for which multiple sex chromosomes are known. Apart from fusions and fissions also other chromosomal rearrangements undoubtedly

Table 2

The number of species with different 2n in 15 families of Fulgoroidea

| Family | Chromosome numbers* (2n) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 35 | 37 |
| Tettigometridae | | | | | | | | 2 | | 1 | | | | | |
| Delphacidae | | | | | | 6 | 1 | 1 | 10 | 2 | 54 | | 3 | 1 | 1 |
| Cixiidae | 1 | | | | | | 1 | | | | 2 | | 1 | | |
| Meenoplidae | | | | | | | | | 3 | | | | | | |
| Derbidae | | | | | | | 1 | | 7 | | | | | | |
| Achilidae | | | | | | 1 | | 1 | 4 | | | | | | |
| Dictyopharidae | | | | | | | | 17 | 11 | | 13 | | | | 1 |
| Fulgoridae | | | | | | | 1 | 2 | 2 | | | | | | |
| Issidae | | | | 1 | | | 1 | | 1 | | | | | | |
| Nogodinidae | | | | | | | | 3 | 1 | | | | | | |
| Tropiduchidae | | | | | | | 2 | | 1 | | 1 | | | | |
| Lophopidae | | | | | | | | | 3 | | 2 | | | | |
| Eurybrachidae | | | | | | | | 2 | 1 | | | | | | |
| Ricaniidae | | | 1 | | | | | | 2 | | | | | | |
| Flatidae | | | | 1 | 1 | 1 | 1 | | 4 | 1 | | | | | |
| Total: 182 | 1 | | 1 | 2 | 1 | 8 | 8 | 28 | 50 | 4 | 72 | | 4 | 1 | 2 |

*2n are given for males. Even 2n are evidenced to the XY sex-determining system in the species, odd 2n to the X0 system.

occurred in the evolution of Fulgoroidea. However, it is nearly impossible to reveal them on conventionally stained holokinetic chromosomes. Modern methods of differential staining have not yet been used for the study of chromosomes in Auchenorrhyncha.

In Fulgoroidea in the total testis structure of 140 species (approximately 1,9% of all known species) belonging to 14 families is known so far (Table 3). The number of follicles varies from 2 to 24 per testis in males (Fig. 37). Variation patterns of this character in the majority of families are not clear,

Table 3

Number of species with particular structure of testes in 14 families of Fulgoroidea

| Family | Number of follicles per testis | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 2 | 3 | 4 | 5 | 6 | 7 | 8/10 | 9 | 10/12 | 11 | 12 | 17 | 20 | 24 |
| Tettigometridae | | 1 | | 1 | 4 | | | | | | | | | |
| Delphacidae | | 29 | | | 3 | | | | | | | | | |
| Cixiidae | 2 | | 4 | 1 | 3 | | | | | | | | | |
| Meenoplidae | | | | | 1 | | | | | | | | | |
| Derbidae | 1 | 1 | 3 | 2 | 1 | | | | | | | | | |
| Achilidae | | 11 | 1 | 1 | 5 | 1 | | | | | | | | |
| Dictyopharidae | | | 22 | | 18 | | | | | | | | | |
| Fulgoridae | | | | 2 | 4 | | | | | | | | | |
| Issidae | | | | | 1 | | | | | 1 | | | 1 | |
| Nogodinidae | | | | 1 | | | | 1 | | | | | | 2 |
| Tropiduchidae | | | | | 3 | | | | | | | | | |
| Lophopidae | | | | | 2 | | | | | | | | | |
| Ricaniidae | | | | | | | | | | 1 | | | | |
| Flatidae | | | | | 1 | | 1* | | 1* | | 2 | 1 | | |
| Total: 140 | 3 | 42 | 30 | 8 | 46 | 1 | | 1 | 1 | 2 | 2 | 1 | 1 | 2 |

*The only studied male of the species displayed the different follicle number in different testes.

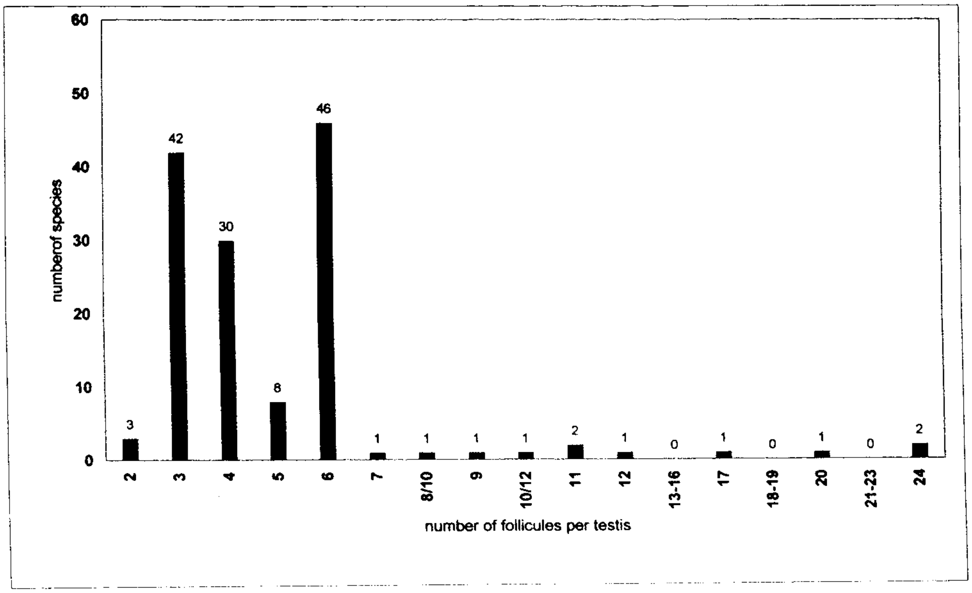


Fig. 37. Histogram showing the frequency distributions of follicle numbers per testis in Fulgoroidea.

except for Dictyopharidae and Delphacidae. In these families follicle number turned out to be relatively stable in genera and tribes. Cixiidae, Derbidae, and Flatidae display notable variation of this character. Possibly this results from the fact that representative data are available for Dictyopharidae and Delphacidae whereas our knowledge of other families is fragmentary.

Predominant in Fulgoroidea are testes consisting of 6, 3, and 4 follicles. Such a testis structure has been found in 37%, 30% and 23% of studied species respectively. The majority of species with 4 follicles per testis belong to Dictyopharidae (22); this follicle number occurs in three other families, although sporadically. Testes consisting of 3 follicles are typical of Delphacidae, where they have been found in 29 out of 32 studied species; this follicle number occurs in three other families, the feature being predominant in Achilidae studied up to the present. Most typical of Fulgoroidea are 6 follicles per testis in males. Such a testis structure has been discovered in the majority of families, although it has not yet been found in Nogodinidae and Ricaniidae. The presented new data support the earlier statement (EMELYANOV & KUZNETSOVA 1983) that 6 follicles per testis is the initial state of this character in Fulgoroidea as a whole. Oligomerization and polymerization of testicular follicles occurred in the evolution of Fulgoroidea. Oligomerization probably being predominant or more successful leading to lower numbers, such as 3 in advanced taxa of Delphacidae, or 4 in advanced taxa of Dictyopharidae. It is interesting to note that high numbers (above 6) have been found so far only in advanced families – Issidae, Nogodinidae, Ricaniidae and Flatidae.

Thus we assume that the common ancestor of Fulgoroidea had 2n = 27, 28 (26+XX/X0) and 6 follicles per testis in males.

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