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Karyotypes and reproductive biology of some mealybugs (Insecta: Coccinea: Pseudococcidae)

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Abstract. The cytogenetic features and some aspects of reproductive biology of 9 species of mealybugs (*Antonina evelynae* Gavrilov, 2003, *Balanococcus singularis* (Schmutterer, 1952), *Coccura comari* (Künow, 1880), *Dysmicoccus multivorus* (Kiritshenko, 1936), *Heterococcus nudus* (Green, 1926), *Phenacoccus aceris* (Signoret, 1875), *Trionymus aberrans* Goux, 1938, *T. haancheni* McKenzie, 1960, and *T. perrisii* (Signoret, 1875)) are presented and illustrated. *B. singularis*, *D. multivorus*, *H. nudus*, and *Ph. aceris* have each 2n=10, *A. evelynae* and *C. comari* – 2n=12, and all three studied *Trionymus* spp. – 2n=16. A part of the embryos of each species had specific heterochromatinization of the haploid paternal set of chromosomes, according to the Lecanoid genetic system. The data on oviposition (oviparity and ovoviviparity), sex-ratios and anatomy of the female reproductive organs are given and briefly discussed.

Key words: scale insects, mealybugs, cytogenetics, chromosomes, karyotypes, sex-ratios, oviparity, ovoviviparity.

Introduction

Pseudococcidae (mealybugs) are one of the biggest scale insect families with approximately 272 genera and 2000 species in the world fauna. It is a fairly diverse group, species of which occupy very different ecological niches from very dry deserts to marshes in the tropical and temperate zones. All the mealybugs are sap-suckers connected with host plants, and there are a lot of species that are dangerous pests of agricultural and ornamental plants, for example, such famous and world wide distributed species as *Pseudococcus viburni* (Signoret, 1875), *Planococcus citri* (Risso, 1813), *P. ficus* (Signoret, 1875), *Saccharicoccus sacchari* (Cockerell, 1895), etc.

The group is characterized (as well as other scale insects) by many peculiar cytogenetic characters: holocentric chromosomes, inverse meiosis, different sex-determining mechanisms and patterns of chromosome behavior in meiosis and mitosis, unique phenomena of "dizygotic soma" and heterochromatinization of the paternal set of chromosomes, male haploidy, facultative and obligate parthenogenesis, and others (Hughes-Schrader, 1948; Brown, 1965; Buchner, 1965; Nur, 1980; Normark, 2001; Kuznetsova, Gavrilov, 2005; Gavrilov, 2007).

Recent catalogue of chromosome numbers of scale insects (Gavrilov, 2007) includes 42 genera and 113 species of Pseudococcidae, i.e. 5.65% of the world fauna of the mealybugs. Diploid chromosome number varies from 8 to 64, with the modal number 10.

Phylogenetic relationships of most mealybug genera are unclear and we hope that the cytoge-

netic data will be useful for further understanding of the macro- and microevolution of the group. Also karyological characters may be useful for taxonomical studies of scale insects (Hughes-Schrader, Tremblay, 1966; Brown, 1965; Cook, 2000, 2001; Gavrilov, 2004; Gavrilov, Kuznetsova, 2005).

This paper presents new data on karyotypes and reproductive biology of 9 species of mealybugs from 7 genera. Chromosome number of *Phenacoccus aceris* (Signoret, 1875) was reported for the first time by Drozdovsky (1966), but without comments and photographs of karyotype. More recently, primary data on chromosome numbers of *Antonina evelynae* Gavrilov, 2003, *Heterococcus nudus* (Green, 1926), *Phenacoccus aceris*, *Dysmicoccus multivorus* (Kiritshenko, 1936), *Trionymus aberrans* Goux, 1938, and *Trionymus perrisii* (Signoret, 1875) were reported by Gavrilov (2004), but also without comments and photographs of karyotypes. All other data, including chromosome numbers of *Balanococus singularis* (Schmutterer, 1952), *Coccura comari* (Künow, 1880) and *Trionymus haancheni* McKenzie, 1960 are given here for the first time. For *B. singularis* and *H. nudus*, the presented data are the first cytogenetic reports for the comparatively large genera *Balanococcus* Williams, 1962 (34 species in the world fauna) and *Heterococcus* Ferris, 1918 (12 species).

The approximate numbers of nominal species and genera are given here and below according to ScaleNet (www.sel.barc.usda.gov/scalenet/scalenet.htm, on November 1, 2007).

Morphological and cytological preparations are deposited in Zoological Institute, Russian Academy of Sciences, St. Petersburg.

Material and methods

All material was collected by I. Gavrilov. The collecting data are following:

Antonina evelynae, K 324, Russia, Krasnodar Krai, Sochi, on stems of *Phyllostachis* sp., 10.V.2003. K 336, the same data, but 17.V. 2003.

Balanococcus singularis, K 433, Russia, Voronezh Province, 5 km E of Grafskaya st., under the leaf sheaths of *Poa* sp., 30.V.2004.

Heterococcus nudus, K 364, Russia, Voronezh Province, 5 km E of Grafskaya st., under the leaf sheaths of *Poa* sp., 14.VI.2003. K 432, the same data, but 29.V.2004.

Phenacoccus aceris, K 346, Russia, Voronezh, forest near "Electronika" hospital, on stem of *Malus silvestris*, 1.VI.2003. K 471, Ukraine, the Crimea, mountain forest above Yalta, on stems and leafs of *Hedera colchica*, 7.VI. 2005.

Dysmicoccus multivorus, K 352, Russia, Voronezh, sandy waste near Mashmet st., on underground stems of *Medicago falcata*, 10.VI.2003. K 373, Russia, Voronezh Prov., Divnogor'e, on roots of *Salvia nutans*, 15.VI. 2003. K 464, Ukraine, the Crimea, mountain forest above Yalta, on stems of *Trifolium* sp., 4.VI.2005. K 472, the same place, but on steams of undetermined herbaceous plant, 7.VI.2005. K 476, the same place, but on stems of *Trifolium* sp., 16.VI.2005.

Coccura comari, K 534, France, 60 km S of Paris, Fontainebleau forest, on stems of *Rubus* sp., 25.V.2007.

Trionymus aberrans, K 288, Russia, Voronezh, sandy waste near "Electronika" hospital, under the leaf sheaths of *Elytrigia repens*, 13.VI.2002. K 502, the same data, but 23.VI. 2006.

Trionymus perrisii, K 284, Russia, Voronezh Province, Divnogor'e, on roots of grass, 11. VI.2002. K 372, the same place, but under the leaf sheaths of *Bromopsis* sp., 15.VI.2003. K 365, Russia, Voronezh Province, 5 km E of Grafskaya st., under the leaf sheaths of *Poa* sp., 14.VI.2003.

Trionymus haancheni, K 548, USA, Illinois,

Shawne Wood Natural Forest, on roots and under the leaf sheaths of grass, 17.VII.2007.

Adult females with ovisacs were fixed in aceto-ethanol (1 : 3) during 24 hours, transferred to 96% ethanol and preserved in refrigerator. The gravid females were dissected under stereoscopic microscope. The preparations were routinely stained using the Feulgen-Giemsa technique by Grozeva and Nokkala (1996): the embryos were squashed in a small drop of 45 % acetic acid. After the removal of coverslips using dry ice, the preparations were dehydrated in fresh aceto-ethanol for 20 min and air-dried. Then the slides were treated in 1 N HCl at the room temperature for 20 min, hydrolyzed in 1 N HCL at 60º C for 7 min, stained with Shiff's reagent for 30 min, and rinsed in distilled water and Sorensen's phosphate buffer pH 6.8 for 5 min in each. Finally, the slides were stained with 5% Giemsa in Sorensen's buffer for 20-30 min. After staining, the preparations were rinsed briefly with distilled water, air-dried, and mounted in Entellan.

C-banding treatment was performed according to Sumner's technique (1972). A part of material was stained by squashing in a drop of lactoacetorsein (50 ml 85 % lactic acid: 2 g orsein: 50 ml glacial acetic acid). The primary sex ratio was revealed by countering of young embryos, squashed in lactoacetorsein.

Results and Discussion

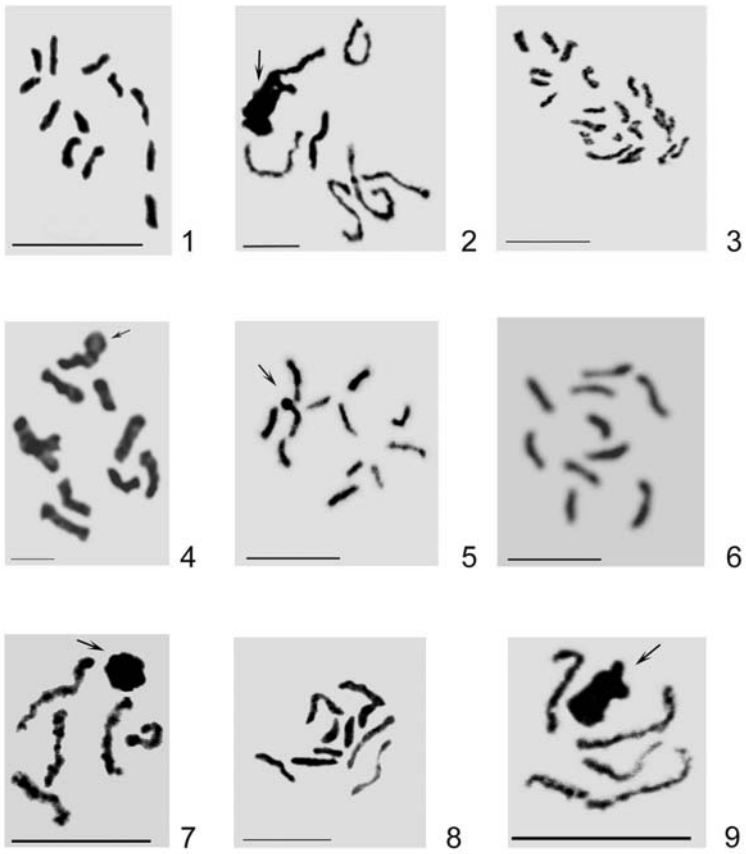
Karyotypes

B. singularis, D. multivorus, *H. nudus*, and *Ph. aceris* have each 10 chromosomes in diploid sets (Figs 4, 6, 8, 10, 21-24), that is the usual (modal) chromosome number for mealybugs (Nur et al., 1987; Gavrilov, 2007). Karyotypes of each of these species consist of chromosomes gradually differing in size, excluding *H. nudus* that has a pair of significantly longer chromosomes. Some embryonic cells of *Ph. aceris* (Voronezh population) had additional chromosome elements (probably, B-chromosomes) (Figs 12-13).

A. evelynae has 12 similar in size chromosomes (Figs 1, 20) in diploid set as well as *A. crawi* Cockerell, 1900, studied by Nur et al. (1987). Two other cytogenetically studied species of the genus, *A. graminis* (Maskell, 1897) and *A. pretiosa* Ferris, 1953, have respectively 2n=16 and 2n=24+Bs (Nur et al., 1987). Such intrageneric variation in chromosome number is rather unusual for mealybugs and can be useful for taxonomical and phylogenetical considerations of the genus. Cells of the embryonal polyploid sector had 4n=24 (Fig. 3). According to the Schrader's hypothesis (Schrader, 1923; see also reviews of Hughes-Schrader, 1948; Brown, 1965; Normark, 2001) these cells originate from the fusion of a "secondary zygote" and polar bodies and give rise to bacteriome or mycetome of adult mealybugs. The tetraploid state of these cells points to the fusion of the secondary zygote (2n) with the first polar body (2n). Another situation takes place, for example, in *Trionymus aberrans* (see below).

C. comari has 2n=12; chromosomes gradually differ in size (Figs 5, 25). Only one species of the genus, *C. suwakoensis* (Kuwana et Toyoda, 1915), with 2n=10, was earlier studied cytogenetically (Nur et al., 1987).

All three species of the genus *Trionymus* Berg, 1899 studied here, *T. perrisii* (the type species of the genus), *T. aberrans* and *T. haancheni*, showed 2n=16, with one pair of longer chromosomes (Figs 14, 17, 19, 26-28). Three previously studied species, *T. caricis* McConnell, 1941 (2n=8), *T. insularis* Ehrhorn, 1916 (2n=10) and *T. longipilosus* De Lotto, 1961 (2n=10), have different chromosome numbers (Nur et al., 1987), but last two species are probably not real *Trionymus* spp., because *T. longipilosus* has very long setae, unusual for the genus, and *T. insularis* lacks tubular ducts. The large and world wide distributed genus *Trionymus* is needed in revision, and



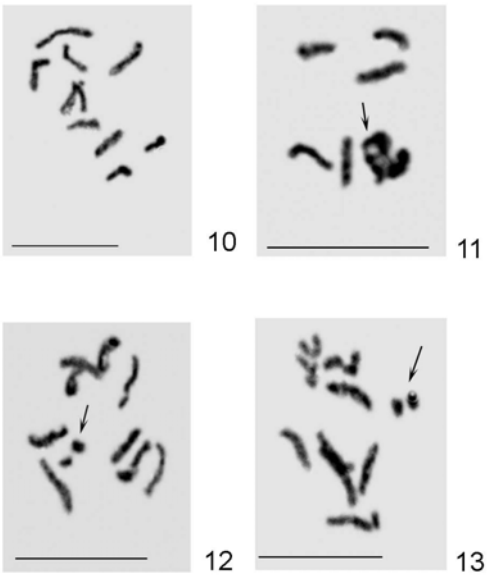
Figs 1-9. Mitotic karyotypes of 5 species of mealybugs. **1-3** - *Antonina evelynae*, 2n=12; **1** - female karyotype, **2** - male, heterochromatinization of paternal set of chromosomes, **3** - cell of embryonal polyploid sector, 4n=24. **4** - *Balanococcus singularis*, 2n=10, female karyotype with nucleolus. **5** - *Coccura comari*, 2n=12, female karyotype with nucleolus. **6-7** - *Dysmicoccus multivorus*, 2n=10; **6** - female karyotype, **7** - male, the heterochromatinization of paternal set of chromosomes. **8-9** - *Heterococcus nudus*, 2n=10; **8** - female karyotype, **9** - male, the heterochromatinization of paternal set of chromosomes. Bar=10 μm.

these two species obviously will be transferred to other genus. Unfortunately, the structure of karyotypes of the three above mentioned species remained unstudied (Nur et al., 1987).

In *T. aberrans*, cells of embryonal polyploid sector (Fig. 15) had 5n=40. So, in contrast to *Antonina evelynae* (see above) these cells have probably originated from the fusion of a "secondary zygote" with two polar bodies: I (2n) and II (n).

Some embryonal cells of *T. aberrans* included 1 or 2 chromosomal fragments in addition to 16 chromosomes of standard karyotype. Also, in one egg we observed meiotic metaphase I with 8 bivalents (Fig. 16).

C-banded karyotypes of *D. multivorus* and *Ph. aceris* revealed small terminal C-bands. This situation is typical for insects displaying holokinetic chromosomes (Kuznetsova et al., 2003) and was also shown for all 3 scale insect species previously studied in this respect (Ferraro et al., 1998; Nechayeva et al., 2004; Gavrilov, Kuz-netsova, 2005).



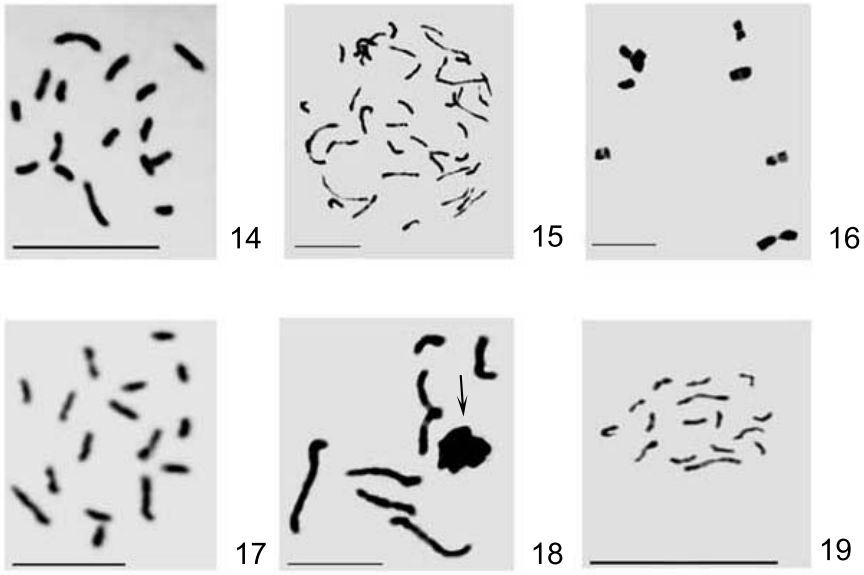
Figs 10-13. Mitotic karyotypes of *Phenacoccus aceris*, 2n=10. **10** - female karyotype. **11** - male, heterochromatinization of paternal set of chromosomes. **12-13** - female karyotypes with additional chromosomes (arrowed). Bar=10 μm.

Nucleoli

The lactoacetorsein staining of embryonic cells demonstrated nucleoli in some plates of *C. comari* and *B. singularis*. In *C. comari* the nucleoli were localized terminally on one homologue of the first chromosome pair (Fig. 5). The same pattern was reported for 3 *Dactylopius* spp. from the family Dactylopiidae (Aquino et al., 1994), for *Rhizoecus mexicanus* (Hambleton, 1946) from Pseudococcidae (Gavrilov, 2005), for *Diaspidiotus gigas* (Thiem et Gerneck, 1934) from Diaspididae (Gavrilov, 2005). Well studied mealybugs *Pseudococcus viburni* and *Planococcus citri* have NORs, located in the middle of the longest chromosome pair (Ferraro et al., 1998; Nechaeva et al., 2004). Two species of soft scales (Coccidae), *Coccus hesperidum* Linnaeus, 1758 and *Saissetia coffeae* (Walker, 1852), studied by Nur (1979) using acetocarmine method, bore nucleoli not far from the end and at the end of one of two longest chromosomes, correspondingly. In *B. singularis* studied here the nucleolus was located at the end of one of short chromosome pairs (Fig. 4) similar to *Acanthococcus insignis* (Newstead, 1891) (Eriococcidae) that demonstrated nucleolus not far from the end of one of the shortest pairs (Gavrilov, 2005). So, till now we have seen various localization of NORs in scale insects, but the available data are not enough for their using in practical taxonomy and for phylogenetic considerations.

Heterochromatinization of the paternal set of chromosomes

A part of the embryos of each species studied here had specific heterochromatinization of the haploid paternal set of chromosomes (Figs 2, 7, 9, 11, 18), according to Lecanoid genetic system that is common for mealybugs (Nur et al., 1987; Gavrilov, 2007). The species with Lecanoid system, as well as with the Comstockioid and Diaspidoid systems have specific heterochromatinization (followed by elimination in two last systems) of the paternal chromosomes in males. Embryonic paternal genome elimination (PGE) is known in some groups of insects (see reviews of White, 1973 and Normark, 2003), but in each of these groups PGE has specific characters and forms unique genetic systems. In the Lecanoid system, the heterochromatic chromosomal set exists over all the stages of the male life cycle. In male meiosis, the chromosomes do not pair and separate equationally during the first division. During the second division, two metaphase plates are formed, and the heterochromatic and euchromatic chromosomes segregate to opposite poles (Hughes-Schrader, 1948; Nur, 1980). As a result of meiosis, quadrinucleate spermatids are formed, but only nuclei of maternal origin produce sperm. Earlier (Nur, 1980) it was postulated that

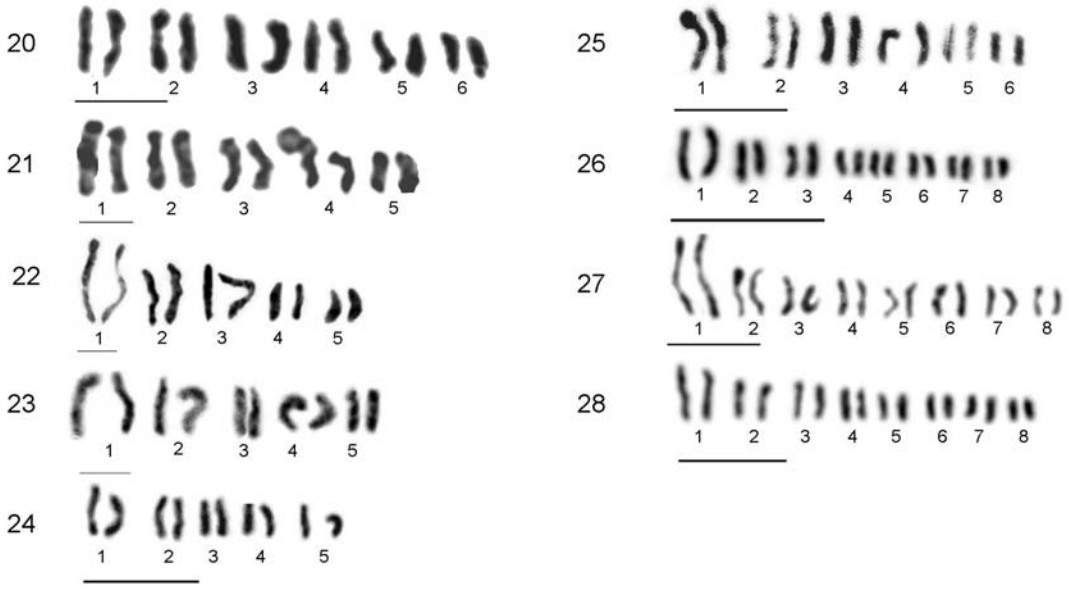


Figs 14-19. Mitotic karyotypes of *Trionymus* spp. **14-16 –** *T. aberrans*, 2n=16; **14 -** female karyotype, **15 -** cell of embryonal polyploid sector, 5n=40, **16 –** meiotic metaphase I. **17-18 -** *T. haancheni*, 2n=16; **17 -** female karyotype, **18 -** male, heterochromatinization of paternal set of chromosomes; **19 -** *T. perrisii*, 2n=16; female karyotype. Bar=10 μm.

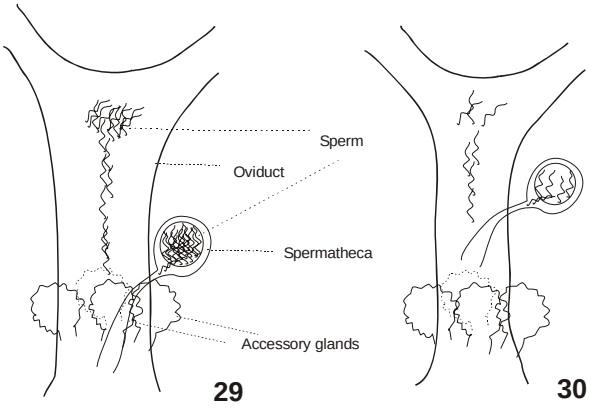
the Lecanoid system (as well as Comstockioid and Diaspidoid systems) must be purely bisexual, but according to a novel approach to the terminology for scale insect genetic systems (Gavrilov, Kuznetsova, 2007), these systems can be also facultatively parthenogenetic. So, species studied in this work have the Lecanoid system, even if some populations or some females of these species reproduce parthenogenetically.

Reproductive biology

We have never seen males of studied species. This situation is usual for scale insects, because in most species males rarely occur and live a short time, often inhabiting other host plants than females. On the other hand, our studies revealed significant portions of male embryos in all studied species (Table), and in all species the primary sex ratio have been differenting more or less from the 1 : 1 (the only studied female of *B. singularis* contained 9 male and 5 female embryos). Scale insects with Lecanoid, Comstockioid and Diaspidoid genetic systems have no chromosomal mechanism of sex determination, and sex of progeny depends on the age of female (time of waiting for fertilization), environmental conditions (Nur, 1990), host plant (for polyphagous species) (Bustshik, Saakyan-Baranova, 1962), etc. However, in obligatorily bisexual species, for example, *P. viburni* or *P. citri*, the average sex ratio is usually close to 1 : 1 (Franco et al., 2000; Nechaeva et al., 2004) and significant deviations from this ratio can point to the probable parthenogenetic reproduction of part or all females. We anatomized reproductive organs of *A. evelynae* (3 females), *D. multivorus* (K 352, 3 females; K 373, 3 females; K 464, 3 females), *T. haancheni* (4 females), *T. perrisii* (K 365, 3 females, K 372, 3 females), and *H. nudus* (K 432, 5 females). In 4 first species spermatheca was found to occupy proximal position (Fig. 29), whereas in *H. nudus* – distal position (Fig. 30) that can be a result of fusion of a part of sper-



Figs 20-28. Karyograms. **20 -** *Antonina evelynae*. **21 -** *Balanococcus singularis*. **22 -** *Heterococcus nudus*. **23 -** *Phenacoccus aceris*. **24 -** *Dismicoccus multivorus*. **25 -** *Coccura comari*. **26 -** *Trionymus aberrans*. **27 -** *T. perrisii*. **28 -** *T. haancheni*. Bar=10 μm.



Figs 29, 30. Spermathecae. **29 -***Trionymus haancheni*. **30 -** *Heterococcus nudus*.

matheca duct with oviduct. All females had sperms in spermathecae and oviducts, but in two last species there were few sperms. So, at least some females of studied species seem reproduce bisexually.

Oviposition and ovoviviparity

The study of gravid females has shown that the oviposition in *B. singularis*, *H. nudus*, *Ph. aceris*, *T. aberrans*, and *T. perrisii* takes place at the stage of invagination of the germ band in the embryo, whereas in *T. haancheni* and *D. multivorus* – at the beginning of (or directly prior to) the formation of antennae and legs. In *A. evelynae* and *C. comari,* almost all phases of the embryo development (including the formation of antennae and legs) occur before oviposition inside the mother's body, and so, we consider these two species as really ovoviviparous. On the other hand, in some cases the stage of embryo development at the time of oviposition may slightly differ in different populations of the same species (as in *D. multivorus*) or even in the same female (as in *T. aberrans*). Unfortunately, the ovoviviparity in scale insects (as also embryology of the group) are very poorly studied and we avoid to give any presumptions here. See also terminological com-

Table. The primary sex ratio in 8 species of mealybugs. Coll. No. – collecting number, embr. – embryos.

Material		Male embr.	Female embr.
Coll. No.	No. ♀		
Antonina evelynae Gavrilov			
K 336	1	2(40%)	3(60%)
	2	2(18%)	9(82%)
	3	2(25%)	6(75%)
	4	13(29%)	32(71%)
	5	10(22%)	35(78%)
	6	12(21%)	44(79%)
	7	14(23%)	48(77%)
	8	22(48%)	24(52%)
Total		77(28%)	201(72%)
Coccura comari (Künow)			
K 534	1	4(24%)	13(76%)
	2	22(27%)	59(73%)
	3	12(21%)	46(79%)
	4	20(31%)	45(69%)
Total		58(26%)	163(74%)
Dysmicoccus multivorus (Kiritshenko)			
K 472	1	18(58%)	13(42%)
	2	6(25%)	18(75%)
	3	20(61%)	13(39%)
	4	20(44%)	25(56%)
	5	21(46%)	25(54%)
	6	17(44%)	22(56%)
	7	16(42%)	22(58%)
	8	10(45%)	12(55%)
Total		128(46%)	150(54%)
K 476	1	4(14%)	25(86%)
	2	20(62%)	12(38%)
	3	6(18%)	28(82%)
	4	22(65%)	12(35%)
	5	11(31%)	25(69%)
	6	15(54%)	13(46%)
	7	13(43%)	17(57%)
	8	15(43%)	20(57%)
Total		106(41%)	152(59%)
K 352	1	12(40%)	18(60%)
	2	10(31%)	22(69%)
	3	19(53%)	17(47%)
	4	12(44%)	16(57%)
	5	11(37%)	19(63%)
	6	17(59%)	12(41%)
	7	13(46%)	15(54%)
	8	12(35%)	22(65%)
Total		106(43%)	141(57%)

ments on the question in this issue (Gavrilov, Kuznetsova, 2007).

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Table (continuation).

Heterococcus nudus (Green)			
K 432	1	24(75%)	8(25%)
	2	29(83%)	6(17%)
	3	30(75%)	10(25%)
	4	25(76%)	8(24%)
	5	24(67%)	12(33%)
	6	18(56%)	14(44%)
	7	14(64%)	8(36%)
	8	22(69%)	10(31%)
Total		186(71%)	76(29%)
Phenacoccus aceris (Signoret)			
K 346	1	10(33%)	20(67%)
	2	22(55%)	18(45%)
	3	18(38%)	30(62%)
	4	25(62%)	15(38%)
	5	9(36%)	16(64%)
	6	24(51%)	23(49%)
	7	14(40%)	21(60%)
	8	17(38%)	28(62%)
Total		139(45%)	171(55%)
K 471	1	7(25%)	21(75%)
	2	17(46%)	20(54%)
	3	16(68%)	8(33%)
	4	10(34%)	19(66%)
	5	14(41%)	20(59%)
	6	10(45%)	12(55%)
	7	8(33%)	16(67%)
	8	12(33%)	24(67%)
Total		94(40%)	140(60%)
Trionymus aberrans Goux			
K 478	1	17(30%)	39(70%)
K 288	1	12(40%)	18(60%)
K 502	1	9(33%)	18(67%)
	2	16(57%)	12(43%)
	3	14(44%)	18(56%)
Total		39(45%)	48(55%)
Trionymus haancheni McKenzie			
K 548	1	13(31%)	29(69%)
	2	-	30(100%)
	3	17(34%)	33(66%)
	4	16(34%)	31(66%)
	5	8(24%)	26(76%)
	6	14(39%)	22(61%)
	7	13(31%)	29(69%)
	8	17(49%)	18(51%)
Total		98(31%)	218(69%)
Trionymus perrisii (Signoret)			
K 372	1	5(17%)	25(83%)
	2	8(27%)	22(73%)
	3	17(44%)	22(56%)
	4	10(29%)	24(71%)
	5	10(33%)	20(67%)
	6	14(44%)	18(56%)
	7	16(57%)	12(43%)
	8	11(38%)	18(62%)
Total		91(36%)	161(64%)

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