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Automictic and Apomictic Parthenogenesis in Psocids (Insecta: Psocoptera)

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Karyotypes and meiosis patterns in three obligatory thelytokous Psocoptera species have been studied for the first time. Females of *Aaroniella badonneli* (Danks) display 9 chiasmatic bivalents in oocyte metaphase I (2n = 18), hence meiosis is of the automictic type. Females of *Ectopsocus meridionalis* Ribaga and *Valenzuela* sp. display 3n = 27, and 27 univalent chromosomes are present in oocyte metaphase I. Thus, meiosis in these species is of the apomictic type.

Key words: Psocoptera, parthenogenesis, karyotype, automictic meiosis, apomictic meiosis.

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Thelytokous parthenogenesis, i .e. a mode of reproduction in which female offspring develop from unfertilised eggs, is well known among insects (WHITE 1973; SUOMALAINEN *et al*. 1987). Two main cytological types of thelytokous parthenogenesis are distinguished – apomixis or ameiotic parthenogenesis, characterized by a single mitotic-like division in unfertilized eggs resulting in genetic identity of the mother and her offspring, and automixis or meiotic parthenogenesis, characterized by normal meiotic reduction of genetic material and subsequent restoration of diploidy in offspring. Both types of parthenogenesis are observed in several insect orders, however, apomixis is more widespread and is referred to as the most common in insects (SUOMALAINEN *et al.* 1987).

Among more than 30 thelytokous species presently known in the order Psocoptera, only four species have been studied cytologically (GOSS 1954; JOSTES 1975; MEINANDER *et al.* 1974; NOKKALA & GOLUB 2002). All of these species have the apomictic type of parthenogenesis (GOSS 1954; NOKKALA & GOLUB 2002).

In the present work the karyotypes and pattern of meiosis in three obligatory thelytokous species, belonging to 3 families of the advanced suborder Psocomorpha, are described for the first time. The automictic type of parthenogenesis is recorded for the first time in Psocoptera.

Material and Methods

Adult females of *Aaroniella badonneli* (Danks) (Psocomorpha, Philotarsidae) were collected during July, 2004 from a natural population inhabiting foliage trees and bushes in North Caucasus, Russia (Krasnodar province, Krasnaja Polyana, 54 km northern Adler, alt. 500, coast of Mzymta river).

Adult females of *Ectopsocus meridionalis* Ribaga (Psocomorpha, Ectopsocidae) were collected during August, 2005 from a natural population inhabiting foliage trees in Hopersky State Reserve, Russia (Voronezh province).

Adult females of *Valenzuela* sp. (Psocomorpha, Caeciliusidae) were collected during July-August, 2004 from several natural populations inhabiting foliage trees and bushes in Reserve “Belogorie”, Borisovka, Russia (during August, 2005 foliage trees in, Russia (Voronezh province).

All specimens were fixed in an ethanol / acetic acid mixture (3:1) and kept refrigerated at 4^{o}C. Mature eggs were extracted from females and placed on slides in a drop of 45% acetic acid. After the chorion was removed, the eggs were squashed and slides were made permanent by a dry-ice technique.

Slides were stained by the Schiff-Giemsa method as described earlier (NOKKALA & GOLUB 2002).

Results

Aaroniella badonneli (Danks) (Philotarsidae), 2n = 18 (16 + XX)

The species is known as obligatory parthenogenetic (LIENHARD 1998).

From 13 females as many as 38 eggs were extracted and examined. A total of 2 pro-metaphases I, 17 metaphases I, and 19 anaphases I were analysed.

Metaphase I displayed 9 bivalents, each with a single terminal chiasma (Fig. 1). The bivalents gradually decreased in size. During anaphase I, half-bivalents segregated to the opposite poles of the nucleus (Fig. 2). The chromosome formula of the species was determined as 2n = 18 (16 + XX).

Ectopsocus meridionalis Ribaga (Ectopsocidae) 3n = 27 (24 + XXX)

The species is known as obligatory parthenogenetic (LIENHARD 1998).

From 15 females as many as 25 eggs were extracted and examined. A total of 25 metaphases were analysed.

Metaphase I displayed 27 univalent chromosomes of different size (Fig. 3). No bivalent formation was observed in mature eggs. The chromosome formula of the species was determined as 3n = 27 (24 + XXX).

Valenzuela sp. (Caeciliusidae) 3n = 27 (24 + XXX)

The species is considered as obligatory parthenogenetic, since no males were found in different populations during two years of sampling.

From the abdomens of 19 females as many as 30 eggs were extracted and examined. A total of 29 metaphases and one anaphase I were analysed.

The counting of chromosomes in M I was difficult, however the total number of elements observed exceeded 20 (Fig. 4). No bivalent formation was observed in mature eggs.

The follicle cells showed 27 chromosomes (Fig. 5), the chromosome formula of the species was therefore determined as 3n = 27 (24 + XXX).

Discussion

The meiosis pattern in diploid obligatory parhtenogenetic *Liposcelis bostrychophilla*, in triploid obligatory parthenogenetic *Valenzuela flavidus*, *Peripsocus subfasciatus* and in diploid facultative parthenogenetic *Thrichadenotecnum majus* was recently described (GOSS 1954; NOKKALA & GOLUB 2002). Apomictic meiosis was established for the above-mentioned species showing a single equational maturation division in the mature eggs.

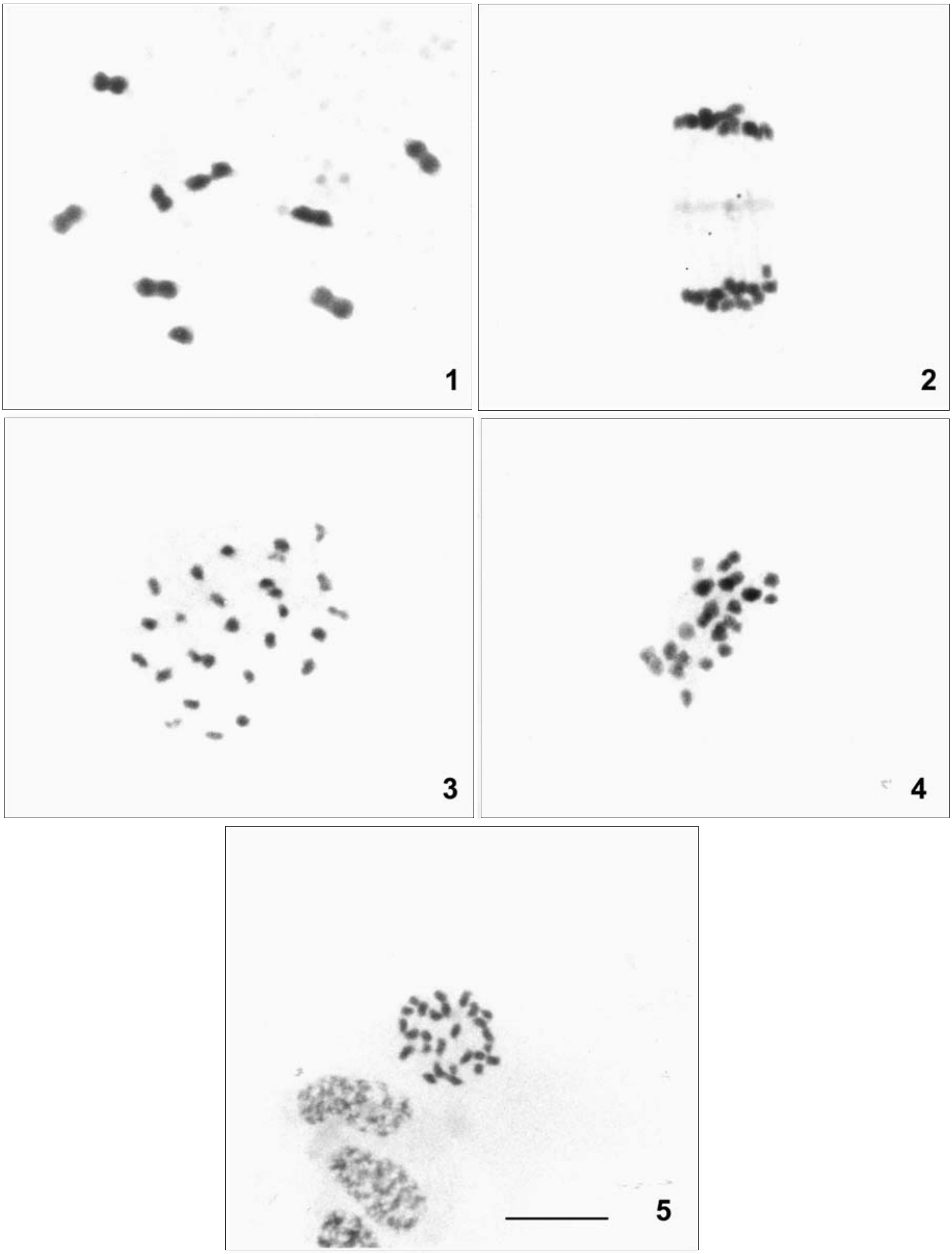
In mature eggs of *E. meridionalis* and *Valenzuela* sp. from the present study a single mitotic-like division occurs indicating an apomictic type of parthenogenesis. On the contrary, the normal meiotic behaviour of chromosomes in mature eggs of *A. badonneli* indicates the presence of an automictic type of parthenogenesis in this species. This finding represents the first example of automixis in Psocoptera as a whole.

Apomixis is considered as a simple mechanism maintaining the ploidy level, while automixis is complicated by various mechanisms of diploidy restoration in offspring. These mechanisms include the premeiotic doubling of chromosomes, the fusion of meiotic derivatives (egg nucleus and second polar nucleus), and different postmeiotic fusions (e.g. fusion of two central polar nuclei, fusion of egg nuclei and a derivative of the first polar body) (SUOMALAINEN *et al.* 1987; KIRKENALL & NORMARK 2003).

Obviously, no premeiotic duplication of chromosomes takes place in *A. badonneli*, displaying orthodox meiotic figures with a haploid number of bivalents in MI. However, the mechanism of ploidy restoration in the offspring remains unknown.

It is generally accepted that automixis is not evolutionarily far from normal meiosis and fertilization (SAURA *et al.* 1993), thus automictic unisexuals can reverse to the normal bisexual state. Conversely, true apomictic parthenogenesis can evolve through the automictic condition and most likely represents a final step in the evolution of thelytokous lineages. The relatively low frequency of automixis among parthenogenetic Psocoptera (1 to 6, compared to apomictic species) may be due to the old age of the order Psocoptera and to the long evolution of parthenogeneitc psocid taxa.

Among paraneopteran (hemimetabolous) insects, to which the order Psocoptera belongs, both apomictic and automictic meiosis were found in parthenogenetic coccids (NUR 1979, 1980), and probably, in parthenogenetic cicadas (DEN BEIMAN 1988; AGUIN-POMBO *et al.* 2005). Parthenogenetic aphids display apomictic meiosis (BLACKMAN 1985), while parthenogenetic aleyrodids and trips have only the automictic type of parthenogenesis (SUOMALAINEN *et al.* 1987).



Figs 1-5. Chromosome complements of 3 parthenogenetic species of Psocoptera. Figs 1-2. *A. badonneli* (Danks). Fig. 1. Oocyte metaphase I with 9 chiasmatic bivalents. Fig. 2. Oocyte anaphase I, showing regular segregation of chromosomes. Fig. 3. *E. meridionalis* Ribaga. Oocyte metaphase I with 27 univalent chromosomes. Figs 4-5. *Valenzuela* sp. Fig. 4. Oocyte metaphase I, showing over 20 univalent chromosomes. Fig. 5. Mitotic metaphase with 27 chromosomes in a follicle cell. Bar = 10 μm.

A. badonneli is characterized by n = 9 (2n = 18). This chromosome number is found in the majority of psocopteran taxa and is considered as a modal number for Psocoptera as a whole (GOLUB 1999). *E. meridionalis* and *Valenzuela* sp. are found to be triploid and display the karyotype 3n = 27, which most likely originated from n = 9. Triploidy is rather common in parthenogenetic animals and dominates over other ploidy levels (SMITH & WIRKKI 1978; SAURA *et al.* 1993). Among groups related to Psocoptera, triploid parthenogenetic species were so far found only in Auchenorrhyncha (DROZOPOULOS 1976; AGUIN-POMBO *et al.* 2005).

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References

AGUIN-POMBO D., KUZNETSOVA V., FREITAS N. 2005. Multiple parthenoforms of *Empoasca* leafhoppers from Madeira Islands. Where are these unisexual forms coming from? J. Heredity (in press).

BLACKMAN R. L. 1985. Aphid cytology and genetics. Evolution and Biosystematics of Aphids. Institute of Zoology, Polish Academy of Science, Warsaw, p. 171.

DEN BEIMAN C. F. M. 1988. Karyotypic variation in besexual species and pseudogamous forms of the planthhopper genus *Ribautodelphax* (Homoptera, Delphacidae). Genetica **76**: 101-110.

DROSOPOULOS S. 1976. Triploid pseudogamous biotype of the leafhopper *Muellerianella fairmairei* Nature **263**: 499-500.

GOLUB N. V. 1999. Review of karyological data in psocids (Psocoptera) and description of karyotypes of 13 species. Entom. Rev. **79**: 412-424.

GOSS R. J. 1957. Ovarian development and oogenesis in the book louse, *Liposcellis divergens* Badonnel (Psocoptera, Liposceliidae). Ann. Entomol. Soc. Am. **47**: 190-207.

JOSTES R. F. 1975. A method for determining the chromosome number of parthenogenetic psocids (Insecta, Psocoptera). Cytologia **40**: 553-555.

KIRKENALL L. R., NORMARK B. B. 2003. Parthenogenesis (In: Encyclopedia of Insects. V. H Resh & R.T. Cardé eds): 851-856. Academic Press.

LIENHARD C. 1998. Psocoptères Euro-Méditerra- néens. Fauna de France 83. Féd. Franç. Soc. Sci. Nat., Paris.

MEINANDER M., HALKKA O., SÖDERLUND V. 1974. Chromosomal evolution in Psocoptera. Notulae Ent. **54**: 81-84.

NOKKALA S., GOLUB N. 2002. Cytogentics of three parthenogenetic Psocid species (Psocoptera, Psocomorpha). Hereditas **137**: 198-201.

NUR U. 1979. Gonoid thelyotoky in soft scale insects (Coccidae: Homoptera). Chromosoma **72**: 89-104.

NUR U. 1980. 7. Evolution of unusual chromosome systems in scale insects (Coccoidea: Homptera). Insect Cytogenetics. Symp. of Royal Ent. Soc. 10. R. L. Blackman, G. M. Hewitt & M. Ashburner eds. Blackwell, Oxford: 97-117.

SAURA A., LOKKI J., SOUMALAINEN E. 1993. Origin of polyploidy in parthenogenetic weevils. J. Theor. Biol. **163**: 449-456.

SMITH S., VIRKKI N. 1978. Coleoptera. Animal Cytogenetics, vol. 5, 366 pp.

SOUMALAINEN E., SAURA A., LOKKI J. 1987. Cytology and Evolution in Parthenogenesis. Boca Tation, F.L.: CRC Press, 216 pp.

WHITE M. J. D. 1973 Animal Cytology and Evolution, 3rd ed. Cambridge University Press, Cambridge, U.K.