

On some terms used in the cytogenetics and reproductive biology of scale insects (Homoptera: Coccinea)

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Abstract. The significance and validity of some terms conventionally used in papers on coccid cytogenetics and reproductive biology are discussed, and some suggestions are made for the terminology to be more correct in describing of remarkable phenomena and processes associated with coccid reproduction and individual development. It is proposed to apply the terms “Lecanoid”, “Comstockiella” and “Diaspidid” referring to the genetic systems of scale insects not only to bisexually reproducing species, but also to parthenogenetic species and populations showing heterochromatinization of paternal set of chromosomes (PGH) during the development of male embryos. It is also proposed to unify the spelling of the above terms as follows: **Lecanoid**, **Comstockioid** and **Diaspidoid**. The classification of the known types of parthenogenesis of scale insects is revised, and the occurrence of facultative and obligatory parthenogeneses is discussed. The existence of true viviparous scale insects is questioned, and the term “ovoviviparity” (instead of “viviparity”) is treated to be the only proper one for all the hitherto studied species with embryonic development inside the mother’s body. The fusions of a cleavage nucleus with polar bodies resulting in the so-called “dizygotic soma” characteristic of the pseudococcid and diaspidid embryonic development is proposed to designate as the “Schrader fusions” in honor of Franz Schrader, the discoverer of this unique phenomenon.

Key words: genetic systems, paternal genome heterochromatinization, parthenogenesis, ovoviviparity.

The cytogenetics of the scale insects has a long history. During nearly 100 years a number of the world’s eminent cytogeneticists were studying the remarkable genetic systems of scale insects and have elaborated the special terminology for different processes and phenomena associated with coccid reproduction and individual development. A review of the considerable literature on the subject and our own studies of many coccid species led the authors to conclude that some terms are incorrect or only partially correct and, additionally, not easily accessible to non-coccidologists.

This paper is aimed to revise, update and unify coccid terminology, and to compare the significance of some terms with analogous ones in other groups of insects. In this paper we shall discuss the basic terminology for (1) genetic systems, (2) parthenogenesis, (3) strategy of birth and (4) “dizygotic” development of scale insects.

Genetic systems

First we have to clarify what we mean by “genetic systems”. In line with Nur (1980), White (1973), and Normark (2003) we treat genetic



system as a combination of sex-determining mechanisms, chromosome behavior in meiosis and modes of reproduction (bisexual, parthenogenetic or hermaphroditic). For details the reader is referred to the authoritative reviews by Hughes-Schrader (1948), Brown (1965), Nur (1980), and Normark (2001) as well as to our review in Russian (Kuznetsova and Gavrilov, 2005). Here we will discuss only the systems with the special paternal genome heterochromatinization (PGH) and elimination (PGE), that is, the systems where the paternal set of chromosomes is rendered inactive in most tissues by heterochromatinization during the development of male embryos. We shall make a brief retrospective journey into the history of names of these systems.

Hughes-Schrader (1948) was the first to classify the coccid genetic systems. Based on 31 species of scale insects studied at that point in time, mainly by her and Franz Schrader, Salli Hughes-Schrader described different forms of parthenogenesis, different special types of meiosis and unique examples of hermaphroditism. In her review, Hughes-Schrader used the term "Lecanoid" meiosis for a type of spermatogenesis discovered in several species of mealybugs (from the genera *Pseudococcus* Westwood, 1840 and *Phenacoccus* Cockerell, 1893), soft scales (from the genera *Coccus* Linnaeus, 1758, *Saissetia* Deplanche, 1859 and *Parthenolecanium* Šulc, 1908), a species of felt scales (*Gossyparia spuria* (Modeer, 1778)) and an unidentified species of the genus *Dactilopius* Costa, 1829. At the time, the above listed groups were classified as a "section Lecanoidae" in contrast to the sections "Margaroidae" and "Diaspidoidae". More recently, Brown (1963, 1965), based on the study of numerous species of armored scales (Diaspididae), coined the terms "Comstockiella" and "Diaspidid" to designate the genetic systems, discovered by him for the first time respectively in the genus *Comstockiella* Cockerell, 1896 and in some genera of the subfamily Diaspidinae. The most comprehensive clas-

sification of coccid genetic systems has been elaborated by Nur (1980), based on his own study and that of earlier workers. In the papers of all the above-mentioned authors the three principal genetic systems, Lecanoid, Comstockiella, and Diaspidid, have originally been considered as bisexual, because all these systems are associated with PGH (Lecanoid) or with PGH followed by PGE (Comstockiella and Diaspidid) that occur during embryogenesis or prior to spermatogenesis. It is necessary at this stage to briefly characterize these systems. In each above system a male develops from a diploid zygote, containing one haploid genome of maternal origin and one haploid genome of paternal origin. However the paternal set of chromosomes becomes heterochromatic and genetically inert in early embryogenesis, hence only the maternal genome is in fact transmitted by the sperm to the next generation. The difference is that in the Lecanoid system the heterochromatic complement is maintained as such during development, whereas in the two remaining systems it is completely (Diaspidid) or partly (Comstockiella) eliminated just prior to the first prophase of spermatogenesis. Of the three systems, the Comstockiella system seems to be the most wide-spread chromosome system in coccids (Nur, 1980).

We emphasize however, that it is far not always easy to unequivocally diagnose just what system is characteristic of a species under study. Further still some species can be equally referred as having one or another system. For example, if males are absent, the genetic system would hence be considered as parthenogenesis. However, it is currently definitely established that many scale insect species combine thelytokous reproduction with amphimixis, producing males amphimictically or parthenogenetically, and parthenogenetically produced males also have PGH/PGE. Moreover, some species variously manifest thelytokous and sexual lineages in different geographical regions or on different host plants. In spite of these facts,

which have already been well known in those days, Nur (1980) classified the systems with PGH/PGE as either purely sexual or parthenogenetic only, then an unequivocal identification of the genetic system in many species is unnecessarily complicated (if not impossible). If one follows the Nur's classification, two or even more genetic systems could be assigned to one and the same species. A curious situation occurs in the family Lecaniidae (currently Coccidae) that according to Nur (1980) does not have Lecanoid system. The solution of the problem is to consider PGH/PGE separately from the mode of reproduction. The PGH is known to constitute a fundamental characteristic of chromosomal behavior in coccid meiosis. It seems to have evolved only once, in the basic phylogenetic line of scale insects (represented by the superfamily Coccoidea), and then three main genetic systems, in order of increasing complexity, sequentially developed on the basis of PGH. Parthenogenesis is in its turn a mode of reproduction, and it has evolved independently in a number of species and has been reported in different coccid taxa (as with or without PGH/PGE). Parthenogenetic lines are known to arise occasionally under certain ecological and geographical factors. Thus, we propose to apply the terms "Lecanoid", "Comstockiella" and "Diaspidid" not only to bisexually reproducing species but also to facultatively parthenogenetic species and populations having PGH/PGE. We find it also necessary to unify the terminology for genetic systems designating them as «Lecanoid», «Comstockioid», and «Diaspidoid», and write these names from the capital letter. This unification will thus allow do not confuse the names of genetic systems with the names of taxonomic groups.

Parthenogenesis

Parthenogenesis where virgin females produce offspring represents one of the common modes of reproduction in insects. For all the groups in which parthenogenesis has been found the reader is

advised to consult White's (1973) review. Suomalainen et al. (1987) described different mechanisms accounting for parthenogenetic development. The most common forms of parthenogenesis are arrhenotoky, deuterotoky and thelitoky. In arrhenotoky, insects are haplodiploid, with haploid males developing from unfertilized eggs while diploid females developing from fertilized diploid eggs. Deuterotoky involves the development of unfertilized eggs in either males or females. Thelitoky is a form of complete parthenogenesis where unfertilized eggs develop in diploid females, therefore, thelitokous species have females only.

Among insects, coccids are well known to have a unique diversity of the types of parthenogenesis (Nur, 1971). Parthenogenetic species and races have been repeatedly described in the families Margarodidae, Pseudococcidae, Coccidae, Asterolecaniidae, and Diaspididae (Hughes-Schrader, 1948; Brown, 1965; Nur, 1971, 1980, 1990; Gavrilov, 2007). In the classification of the types of parthenogenesis the following characters are conventionally used: the mode of reproduction (obligatory = permanent, and facultative), the sex of progeny (arrhenotoky, thelytoky, and deuterotoky) and some fundamental cytogenetical traits (generative = haploid, and somatic, that is in turn subdivided into apomictic and automictic). However, in scale insects some complicated patterns of parthenogenesis occur that embarrass the classification. Many authors have attempted to classify coccid parthenogeneses (Thomsen, 1927; Hughes-Schrader, 1948; Nur, 1971, 1972, 1980). In the most recent classification (Nur, 1980) several types of parthenogenesis are recognized based on 1) sex of progeny; 2) ploidy of males (haploid and diploid arrhenotoky); 3) number of chromosomes in oogonia and in the first metaphase of oogenesis (gonoid and agonoid thelytoky); each of the two last types is additionally subdivided into subtypes based on the mechanism of diploidy restitution. Nur (1980) rejected such traditional terms as "obligatory" and "facultative" parthenogenesis



since in many parthenogenetic scale insects males are sometimes present but do not participate in fertilization. He also rejected the terms “meiotic” and “ameiotic” parthenogenesis since, according to his studies (Nur, 1979), some parthenogenetic species, even though they show no pairing of chromosomes in meiosis, have however two divisions – reductional and equational. Therefore, Nur (1980) proposed to replace these terms by some alternative terms – “gonoid” and “agonoid” thelytoky, which we have mentioned above. These innovations, however, can not be considered appropriate.

Firstly, without a special sophisticated investigation, it is difficult to say with certainty whether a species has an obligatory or facultative parthenogenesis. It seems quite clear that only few species with obligatory parthenogenesis occur in Coccinea. The evidence for this view is that in the Nur's (1990) list all species considered as obligatory parthenogenetic, have in fact a mixed reproductive strategy and include both parthenogenetic and bisexual forms associated with different host plants. The taxonomical status of these forms, whether or not they represent separate species, has been repeatedly discussed in the literature (see Nur, 1990), but still remains disputable. For example, European species *Marchalina hellenica* (Gennadius, 1883) (Margarodidae) was reported as obligatory thelytokous because males are absent (Hovasse, 1930), and females have no spermatheca (Marzo et al., 1990). The males are however claimed to occur in some regions (S. Drosopoulos and Ch. Hodgson, personal communications). Males were also found in *Marchalina caucasica* Hadzibeyli, 1969, which is considered as a synonym of *M. hellenica* (Jashenko, 1999).

Secondly, the very existence of chromosomal reduction in oogenesis is sufficient to classify the parthenogenesis as that of meiotic type. It is presently widely known that in many insects bivalents are formed, however crossing-over is absent, and meiosis is achiasmatic (White, 1973). Parenthetically,

it should also be mentioned that achiasmatic meiosis occurs in many insect orders, e.g. Mecoptera, Orthoptera, Trichoptera, Lepidoptera, Heteroptera, Diptera and Coleoptera, however has never been evidenced for Coccinea and other homopteran insects.

Thirdly, the formation of bivalents is thought to be important for regular segregation of homologues in anaphase, and the lack of chromosome pairing in coccid meiotic prophase (Nur, 1979) is then the phenomenon calling for further investigation.

Finally, discarding of traditional terminology together with the invention of new terms would act as a barrier to communication between coccidologists and specialists on other groups having similar reproductive strategies, including parthenogenesis. It should be added that based on the Nur's (1980) terminology, several types of parthenogenesis could be attributed to a species, for example to *Coccus hesperidum* Linnaeus, 1758, which, according to Nur (1979, 1980), has apomixis and amphimixis, gonoid and agonoid thelytoky.

Thus, we suggest to recognize obligatory and facultative parthenogenesis; use only conventional terminology for parthenogenesis (arrhenotoky, thelytoky and deuterotoky, meiotic and ameiotic parthenogenesis), and reject the terms gonoid and agonoid thelytoky.

Strategy of birth

There are three known strategies of birth such as oviparity, ovoviviparity and viviparity, and all of these occur in insects. Oviparous insects lay eggs with little or no embryonic development within the mother's body. In ovoviviparity, eggs remain within the mother's body until they hatch or are about to hatch. Ovoviviparity differs from viviparity in that the ovoviviparous embryos are nourished by the egg yolk rather than the mother's body. Ovoviviparity is displayed by many insects and is suggested to be widely distributed among Coccinea, however only few publications deal with this pheno-

menon in scale insects (Hagan, 1951; Koteja, 1990; Tremblay, 1997). As is customary when coccidologists describe species, they use the terms “viviparity” and “ovoviviparity” without comments and probably without clear understanding differences between these two terms. Hagan (1951) in his famous fundamental monograph gave a clear definition of the ovoviviparity to distinguish it from viviparity: “The egg contains sufficient yolk to nourish the embryo until hatching and maternal deposition of offspring. No special nutritional structures are developed”. Yet another important character of the ovoviparous development is the presence of a clearly visible chorion covering the egg. Everything considered, all hitherto studied scale insects are ovoviviparous. Tremblay (1997) hold the same viewpoint regarding soft scales and scale insects in general. Alternatively, Koteja (1990), based on Buchner’s (1965) anatomical studies of *Stictococcus* and *Amiomorpha* species, made a conclusion that “distinction between oviparity and ovoviviparity is not clear” and speculated that the above species are viviparous and receive nourishment from the mother’s body. However, Buchner took an interest in endosymbionts, but not in the mode of embryonic development of the species under investigation, therefore, additional studies are required to solve the problem. Based on the current knowledge on the subject and our own data on more than 100 species from 9 families (unpublished), the eggs of scale insects always have both chorion and yolk, so they are clearly ovoviviparous. We cannot exclude, however, that during further investigation of scale insects, especially from the tropics, species with true viviparity will be discovered. So long as the issue remains open, while making the preparation of scale insects, special attention should be given to stage of the egg development inside the mother’s body and to the presence of chorion and yolk in the eggs. This evidence may have important implications for both general biology of scale insects and taxonomical conclusions (Williams, 1985; Danzig, Gavrilov, 2005).

Dizygotic development

Some scale insects are characterized by a very specific pattern of individual development that bears some similarity to a “double” fertilization resulting in the formation of triploid endosperm in the angiospermous plants. In species of the coccid families Pseudococcidae and Diaspididae an embryo is known to develop from two different cells. One of these cells is a normal diploid zygote that gives rise to the majority of insect tissues. The other cell is a polyploid secondary zygote that results from the fusion of a cleavage nucleus with polar bodies. The secondary zygote gives rise to a polyploid bacteriome, or mycetome. Thus, in the latter, each cell includes a haploid set of paternal chromosomes and several maternal complements (Schrader, 1923; Hughes-Schrader, 1948; Brown, 1965; Normark, 2001).

It is surprising, however, that there is no special term for cytogenetic processes followed by the formation of “dizygotic” soma. The absence of such term renders it difficult to discuss this special evolutionary pattern in scientific and, especially, educational papers and books, and also the communication with other biologists. Here, we propose to designate fusions between a cleavage nucleus and polar bodies in the course of pseudococcid and diaspidid embryonic development as “Schrader fusions” in honor of the outstanding geneticist Franz Schrader, the discoverer of this unique phenomenon.

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