

TRUE PARTHENOGENESIS FOR THE FIRST TIME DEMONSTRATED IN PLANTHOPPERS (*HOMOPTERA, DELPHACIDAE*)

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Summary. — True parthenogenesis in planthoppers (*Delphacidae*) is reported for the first time. The parthenogenetic population was found in Greece and appeared to consist of triploid females ($3n=44$) which morphologically are closely related to *Delphacodes* species. Despite their parthenogenetic nature the females responded strongly to acoustic calling signals of males of *Delphacodes capnodes* and subsequent mating resulted in successful insemination. The taxonomic status of this parthenogenetic form is discussed. A formal naming is considered premature and a provisional designation as "*Delphacodes spec. cf. capnodes* (triploid, parthenogenetic)" is suggested.

Résumé. — L'existence d'une parthénogénèse vraie est rapportée pour la première fois chez les Delphacides. La forme parthénogénétique, trouvée en Grèce, est représentée par des femelles triploides ($3n=44$) dont la morphologie ressemble à celle des espèces de *Delphacodes*. Malgré leur nature parthénogénétique, les femelles répondent fortement aux signaux acoustiques des mâles de *Delphacodes capnodes*, et l'accouplement qui s'ensuit aboutit à une insémination réussie. La position taxonomique de cette forme est discutée. Pour l'instant une dénomination formelle est considérée prématurée et cette forme est nommée provisoirement comme suit : « *Delphacodes spec. cf. capnodes* (triploïde, parthénogénétique) ».

Usually the mode of reproduction in planthoppers (*Delphacidae*) is biparental and the sex ratio of field populations is about 1:1. However, research on populations exhibiting aberrant sex ratio's has revealed that also uniparental forms occur. When studying a population of *Muellerianella fairmairei* (Perris) which had a strongly female-biased sex ratio, Drosopoulos (1976) found that part of the population consisted of triploid females producing triploid eggs. The remaining part of the population consisted of about equal numbers of diploid males and females. The triploid females appeared to reproduce by pseudogamy, which means that they need to be inseminated by males in order to initiate the development of their eggs, but the sperm does not contribute to the embryo's genome and the offspring produced is again exclusively female and triploid. Genetically this mode of reproduction is similar to parthenogenesis, ecologically it requires the coexistence with males of a related biparental species. Since then more cases of

pseudogamy have been found in the planthopper genera *Muellerianella* and *Ribautodelphax* (Drosopoulos, 1983; den Bieman, 1984 and in prep.).

A most intriguing case was encountered in Greece where a planthopper population was found, probably belonging to the genus *Delphacodes*, which seemed to consist exclusively of females. Despite extensive sampling no males were found, whereas numerous females could be collected. If males indeed were absent in this population it might be a case of true parthenogenesis. In the whole infra-order of Auchenorrhyncha only one instance of parthenogenesis was found so far, viz. in the cicadellid genus *Agallia* (Black & Oman, 1947).

Alternatively, the possibility of reproduction by pseudogamy had to be studied experimentally, although the absence of males in the field population constituted a practical difficulty. In Greece the genus *Delphacodes* is represented by four biparental species (Drosopoulos *et al.*, 1985), but unfortunately no populations were available from the area where the all-female population was found. As possible substitute mating partners only males from a Dutch population of *D. capnodes* (Scott) could be obtained.

In the few cases known so far, pseudogamy in planthoppers was always coupled with triploidy, and consequently it also seemed useful to analyse the karyotype of the females.

A further problem concerned the taxonomic placement of this population. Morphologically the females showed large similarity with several *Delphacodes*-species, among which *D. capnodes*. Unfortunately however, as reviewed by Asche & Remane (1983), there are no reliable diagnostic characters available to distinguish the females of these species. In such situations comparative studies of acoustic signals, which serve for mate recognition, may be helpful in clarifying the taxonomic identity of closely related species and populations (see e.g. Claridge, 1983). In this case, a study of acoustic behaviour seemed particularly interesting in view of the possibility that this population might be parthenogenetic and then would not be dependent on any form of mate recognition.

Materials and methods

The all-female *Delphacodes*-population was found living on *Carex riparia* Curtis in a wet biotope near Prassino, Nomos Florina, Greece on 1-IX-1983 (see also Drosopoulos *et al.*, 1985). Numerous planthoppers, adults and larvae, were collected and transferred to the laboratory and kept alive on shoots of their field host-plant. However, *Carex riparia* proved to be difficult to rear in the greenhouse, but fortunately, oats (*Avena sativa* L.) was accepted as a suitable substitute host-plant. The planthoppers were reared on two-months old plants at 20 °C and long-day conditions (18 hours light).

For comparative experiments on acoustic and mating behaviour only a Dutch population of *D. capnodes* was available. This population was living on *Eriophorum angustifolium* Honckeny at Tongerense heide, Gelderland, The Netherlands, and could be reared both on *E. angustifolium* and oats. The planthoppers used for the experiments on mating and acoustic behaviour were 7 to 9 days old, and males and females were kept separated since their final larval stage. For the mating experiment in each of four trials ten males and ten females were confined in a cage with oats. After ten days the females were dissected and their spermathecas examined for the presence of sperm.

The substrate-borne acoustic signals of the planthoppers were recorded by the method described by de Vrijer (1984). All recordings were made at 20 °C using stems of *Agrostis capillaris* L. (= *A. tenuis*) as recording substrate.

To assess the karyotype of the populations chromosome preparations of eggs and testes were made. Eggs were treated following the method of Booy (1982). The chorion was removed after a 30-minute treatment with 50 % propionic acid and the swollen yolk-mass was stained in lacto-acetic orcein. Squash preparations of testes were made after fixation in Carnoy and stained with 0.4 % cristal violet.

RESULTS

Mode of reproduction and karyotype

In the breeding experiment the females, sampled from the all-female *Delphacodes*-population in Greece, appeared to be able to reproduce for more than ten generations in the complete absence of males. Although each generation was carefully screened no single male was found among their progeny. These results amply demonstrate that this population reproduces by true parthenogenesis.

After being confined with males of *D. capnodes* for ten days, all females ($n=40$) appeared to be inseminated. Their progeny again consisted exclusively of females.

Of ten field collected females the karyotype was examined on the basis of ovarian eggs, and appeared to be characterized by 44 univalents (fig. 1). Also the progeny of the females inseminated by *D. capnodes*-males was examined and their chromosome number again was 44 ($n=40$ females). In contrast to this, females of *D. capnodes* appeared to have 30 chromosomes paired as 15 bivalents in the Metaphase-I configuration, which is the normal situation found in Delphacids (Halkka, 1959). The males of *D. capnodes* are characterized by a chromosome number of 29, arranged as 14 bivalents and one univalent, indicating a XO-system of sex determination. The karyotype of the all-female population thus seems to be triploid, consisting of two female genomes ($28+2X$) and one male genome ($14+0$).

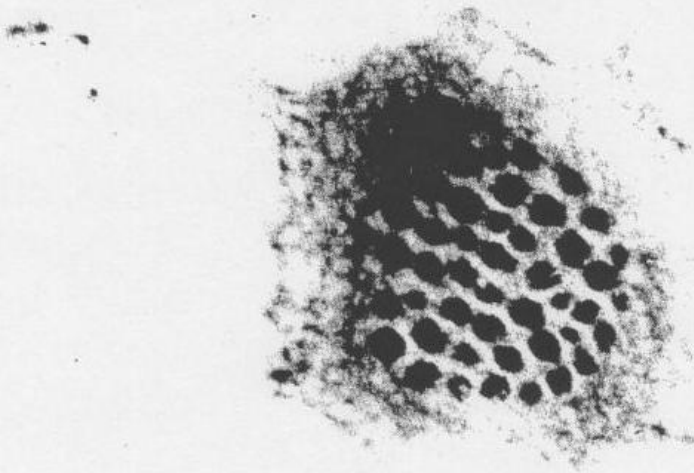


Fig. 1. Metaphase I plate of an ovarian egg of a parthenogenetic *Delphacodes* female, with 44 chromosomes seen in polar view.

Mating and acoustic behaviour

The mating behaviour of the parthenogenetic form subsequently was studied in more detail and compared to that of *D. capnodes*-females. Simultaneously, the acoustic communication between male and female was recorded.

In general, the parthenogenetic form behaved largely similar to the *D. capnodes*-females. In both cases male and female exchanged only a few vibration signals and subsequently copulated very soon after they had been placed together. The duration of the copulation time varied between four and ten minutes for both groups. Termination of the copulation was always initiated by the female, thereby often using her hindlegs and pushing the male away.

The form of the female vibration signals was of the type that seems to be characteristic for Delphacids, viz. a series of regularly repeated "clicks". Again the similarity between the parthenogenetic form and *D. capnodes* was large. As discussed by de Vrijer (1984), comparing acoustic signals emitted during courtship has certain limitations because of the mutual interference of both mating partners. For instance,

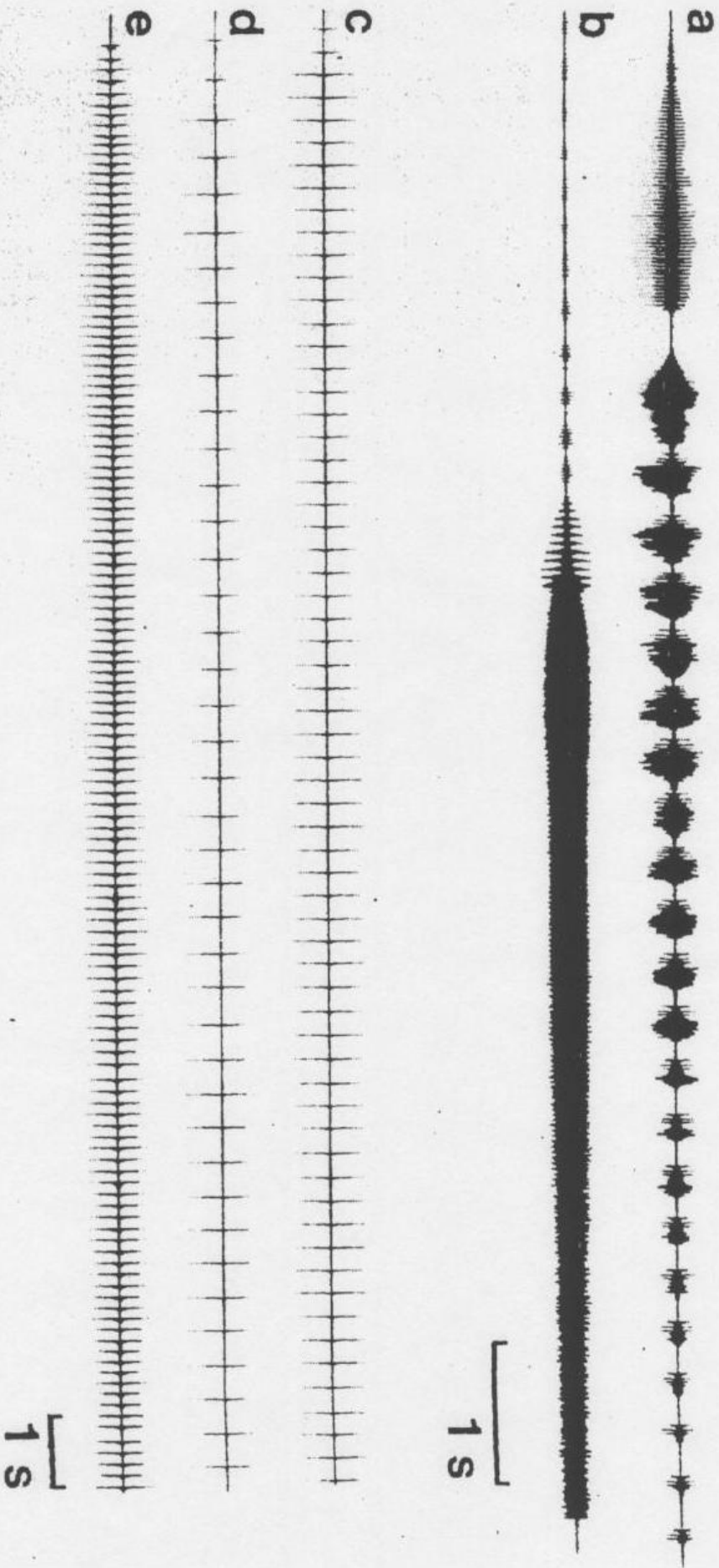


Fig. 2. Temporal pattern of male (a and b) and female (c, d and e) vibration signals in *Delphacodes*: *D. capnodes* (a and c), *D. venosus* (b and e), and the parthenogenetic form (d).

the duration of the female signals could not be assessed properly because of interrupting male calling signals. Only a few registrations of non-interrupted female vibration signals could be obtained through artificial stimulation of isolated females by playback of a recorded male calling signal (see fig. 2a). It appeared that both in *D. capnodes* and in the parthenogenetic form females produce vibration signals of variable length, ranging from one to twelve minutes.

A second parameter, that proved to be better measurable from the courtship recordings, was the "click repetition rate". For both groups of females the values of the click repetition rate were fairly constant and showed little variation. The average values for individual females ranged from 1.9 to 3.3 clicks per second.

DISCUSSION

As clearly follows from the rearing results, the all-female "*Delphacodes*"-population found in Greece reproduces by true parthenogenesis. Analysis of their karyotype further revealed that the females are triploid ($3n=44$). In Delphacidae triploidy until now was only found in pseudogamous forms, although not (yet) in the genus *Delphacodes*. Surprisingly, it was observed that the parthenogenetic females responded acoustically to males of *D. capnodes* and even copulated with them and were inseminated. The progeny of these inseminated females again was all-female and triploid, which is similar to what happens in pseudogamous forms, but contrasts with findings in other groups of animals. For instance, in lizards (Lowe *et al.*, 1970; Bogart, 1980), fishes (Schultz, 1980), and Lepidoptera (Astaurov, 1972) insemination of triploid parthenogenetic forms resulted in offspring with a higher ploidy level.

Also the high percentage of successful insemination by males of the Dutch population of *D. capnodes* is remarkable. In pseudogamous forms comparable high insemination levels were only observed when the females were mated with males of the species with which they were associated in the field. Matings with males of other congeneric species were always less successful (den Bieman, in prep.).

Although the similarities in mating and acoustic behaviour between *D. capnodes* and the parthenogenetic form are considerable, they remain difficult to evaluate without further knowledge about the female signals of other related species. For comparison only unpublished data of one of the other *Delphacodes*-species were available. It concerns recordings of a population of *D. venosus* (Germar) from Finland (leg. R.H. Cobben), of which both the male and female vibration signals appear to be different from those of *D. capnodes* (see fig. 2). The most obvious difference in the female vibration signals is found in the click repetition rate (at 20 °C) which ranged for *D. venosus*-females from 6.1 to 7.6 clicks per second.

Although definite conclusions should not be drawn before also other related taxa have been studied, there are at least strong indications that the parthenogenetic form has evolved from a *D. capnodes*-like ancestor. Whether its triploidy is of an autoploid nature or originated through hybridization with a second species, we can only speculate at this moment.

Considering further the points of similarity with pseudogamous forms, as mentioned above, parthenogenesis might have developed via an ancestral stage of pseudogamy. From an ecological point of view this would mean that the population has freed itself from the obligatory coexistence with a biparental species.

The taxonomic placement of this parthenogenetic form within the genus *Delphacodes*, on the basis of its morphology, seems well in correspondence with its successful mating with *D. capnodes*-males. A further specification of its taxonomic position, however, appears to be difficult. One may argue that this parthenogenetic form is anyhow reproductively isolated from all biparental species known so far, and consequently constitutes a new species. However, within the genus *Delphacodes* two species, *D. mulsanti* (Fieber), from France, and *D. ornatipennis* (Haupt), from Israel,

appear to be described on the basis of female specimens only. According to Asche & Remane (1983) the validity of these descriptions is difficult to assess by lack of reliable diagnostic characters in *Delphacodes*-females. There is, however, a possibility that either or both of these species were in fact parthenogenetic forms with which the population reported here might be conspecific. Unfortunately, this cannot be verified anymore, and thus we are left with two formal but unusable names. At this stage, however, a decision on the formal designation of the parthenogenetic form seems to be premature. First more information should be available on its distribution and its relation to other taxa of the genus. For the moment, the most practical solution seems to be to indicate this form provisionally as "*Delphacodes spec. cf. capnodes* (triploid, parthenogenetic)".

The lack of reliable diagnostic characters in *Delphacodes*-females is a serious obstacle to adequately assess the distribution of the parthenogenetic form. If no males are found, identification remains practically impossible without further experimental research on living specimens. Already there have been reports on pure-female populations of *Delphacodes* by Lauterer (1980) in Czechoslovakia, and by Remane (pers. comm.) in W. Germany.

In view of the few number of genera studied so far, an impressive number of uniparental forms have been recognized in planthoppers during recent years. We may therefore assume that the phenomena of parthenogenesis and pseudogamy most probably will be found in other genera as well. The most effective way to trace new cases is to select field populations on the basis of female-biased sex ratio's for subsequent analysis of the female karyotype and breeding experiments.

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Note : A copy of the original recordings of the vibration signals published in this paper may be obtained by sending a blank audio cassette to the author's adress.

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