

How gynandromorphs arise in Hymenoptera, with two new records from the family Ichneumonidae

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KEY WORDS

Development, female-male mosaic, haplodiploidy, reproductive mode, sex determination

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Gynandromorphs are individuals with both female and male characteristics that occasionally occur in animals. We report the finding of a gynandromorphic specimen in two ichneumonids, *Dicaelotus montanus* and *Sussaba cognata*. Gynandromorphs are the result of developmental aberrations and are often mosaics of female and male tissues. We present four possible causes for gynandromorphism in haplodiploid hymenopterans. We do not know the precise cause of gynandromorphism in the two specimens reported here, as it is not easy to distinguish between these possible causes. *Dicaelotus montanus* is new for the fauna of the Netherlands.

Introduction

The incentive to write this manuscript came from a photo (figure 1a) sent by the second author to the first author. The photo depicts a gynandromorphic specimen of the ichneumonid *Dicaelotus montanus* (De Stefani, 1885). The specimen has a female head but male genitalia. The second author had another gynandromorphic specimen, of *Sussaba cognata* (Holmgren, 1858) (figure 1b), in his collection. A lively e-mail exchange followed between both authors on the possible causes for these aberrant specimens. We decided to write this up in this article.

Gynandromorphs are individuals that contain both female and male characteristics. They are occasionally being found among many organisms, including birds (Chue & Smith 2014), lizards (Mitchell *et al.* 1978) and fish (O'Farrell & Peirce 1989), and appear particularly abundant in arthropods (Narita *et al.* 2010). These last authors list over 250 insect species comprising thirteen orders, including Diptera, Lepidoptera and Hymenoptera, for which gynandromorphs have been reported. They have however also missed several publications (e.g. De Jong 1982, Vlug 1982) and many additional species have been reported since (e.g. Smits *et al.* 2021, Witmond *et al.* 2011). We add the ichneumonids *D. montanus* and *S. cognata* to the list of species for which gynandromorphs have been reported in Hymenoptera (figure 1).

New gynandromorphic ichneumonids

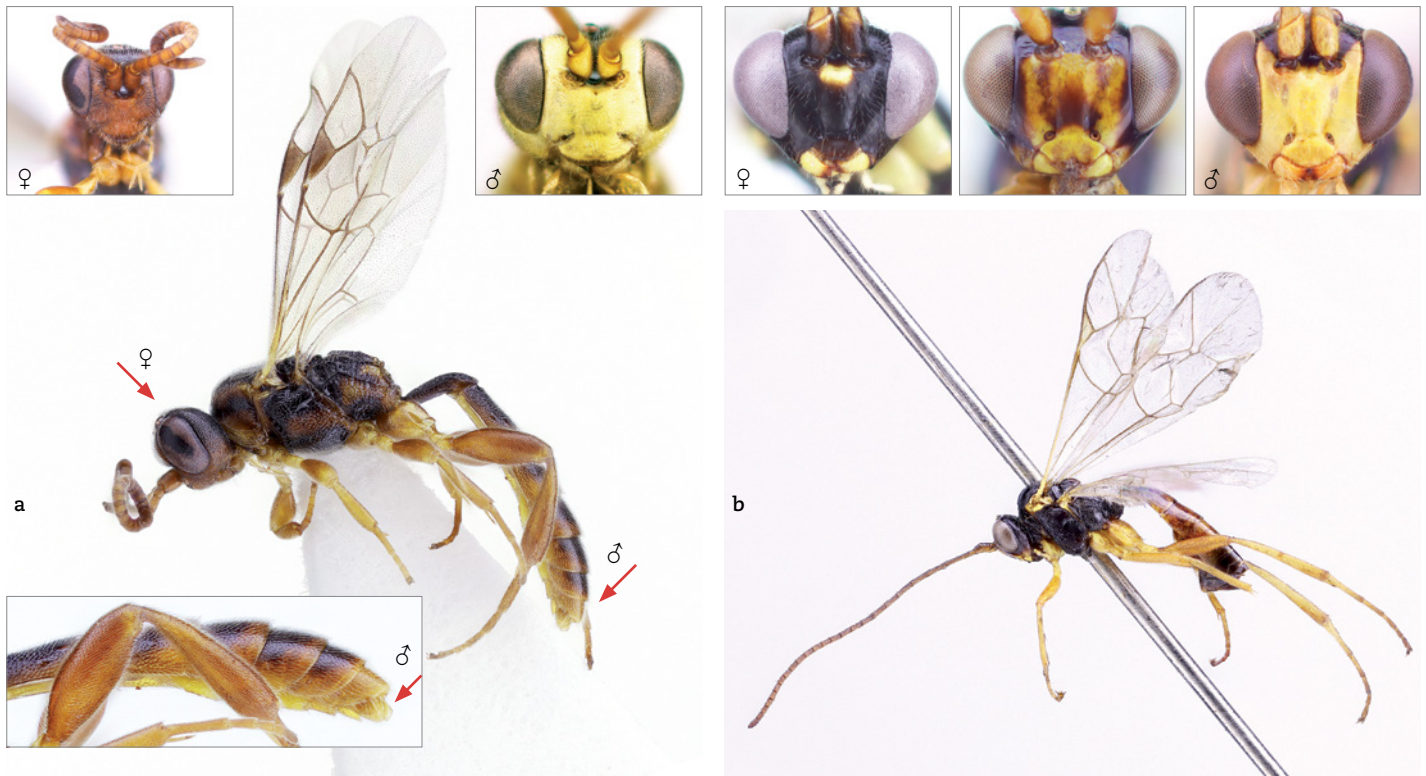
Dicaelotus montanus belongs to the tribe Phaeogenini of the subfamily Ichneumoninae. As such it is likely to be a solitary endoparasitoid of Lepidoptera larvae or pupae, in this case of 'Microlepidoptera'. Ichneumoninae parasitoid imagos always emerge from the host pupa.

The oxygygous metasoma suggests that *D. montanus* oviposits into a young pupa rather than a larva (Hinz 1983) but no host is known. The specimen was collected by Dick Belgers in Wageningen (province of Gelderland) on July 6, 2020 and identified by E. Diller, Zoologische Staatssammlung München. This species is new for the fauna of the Netherlands. The pictured gynandromorphic specimen (figure 1a) has a female head and a male abdomen tip.

Sussaba cognata belongs to the subfamily Diplazontinae. As such it is a solitary koinobiont larval-pupal endoparasitoid of aphidophageous Syrphidae (Diptera). The head of the depicted gynandromorph (figure 1b) is a mixture of the black female and the yellow male form. The antennae are also intermediate between female and male in colour and morphology. The second author collected the specimen September 10, 1973 in Asperen (province of Gelderland).

Reproductive mode and sex determination

Gynandromorphs are aberrant individuals that arise from errors during development. They are most often sexual mosaics or chimerics, carrying both female and male characteristics. Gynandromorphs should not be confused with hermaphrodites, which are individuals that have full female and male function, but these are very rare in insects. To understand how insect gynandromorphs arise requires knowledge about reproductive mode and sex determination. Gynandromorphs can in turn be instructive for elucidating sex determination mechanisms (Zou *et al.* 2020). Gynandromorphs often attract attention, for example Nieuwenhuijsen (2012) considered possible causes for gynandromorphism in two specimens of the solitary bee *Megachile pilidens* Alfken, 1924 using information about developmental biology presented in Ouweneel (1975).



1. Two new gynandromorphic Ichneumonidae (Hymenoptera). (a) *Dicaelotus montanus* and (b) *Sussaba cognata*. The *D. montanus* specimen (a) has a female head and a male abdomen tip. The inserts show the heads of a female (top left panel) and a male (top right panel) and the male abdomen tip (bottom panel). The rest of the body does not show sex specific characters. The *S. cognata* specimen (b) has a gynandromorphic head (top middle panel) compared to the female head (top left panel) and the male head (top right panel). Photos: Kees Zwakhals

1. Twee nieuwe gynandromorfe Ichneumonidae (Hymenoptera). (a) *Dicaelotus montanus* en (b) *Sussaba cognata*. Het *D. montanus*-exemplaar (a) heeft een vrouwelijke kop en een mannelijk achterlijf. De ingevoegde panelen tonen een kop van een vrouwtje (linker bovenpaneel) en een mannetje (rechter boven paneel) en het mannelijke abdomen (bodempaneel). Het *S. cognata*-exemplaar (b) heeft een gynandromorfe kop (midden boven paneel) in vergelijking tot de vrouwelijke kop (linker bovenpaneel) en de mannelijke kop (rechter bovenpaneel).

Upon considering the underlying developmental causes of gynandromorphism, a first distinction needs to be made between diplo-diploid and haplo-diploid species. In diploid species both sexes are diploid, they carry two copies of each chromosome, except for the sex chromosome pair. One of the sexes carries two similar sex chromosomes and the other sex two different ones (figure 2a) or only one copy of the sex chromosome (figure 2b). Under male heterogamety, the male carries an XY pair and the female two X chromosomes. This system is abundant in for example flies and mosquitoes (Diptera) and net-winged insects (Neuroptera) (Beukeboom & Perrin 2014). In some groups, for example grasshoppers and crickets (Orthoptera), the male carries only one X chromosome and no Y (so-called XO or Xzero system). Under female heterogamety, it is the female that carries two different sex chromosomes (referred to as ZW to distinguish from male heterogamety) and the male is ZZ (figure 2c). This is the sex determination system of butterflies and moths (Lepidoptera) and caddisflies (Trichoptera) (Beukeboom & Perrin 2014). Gynandromorphic diploid individuals are often mosaics of XX and XY or ZZ and ZW cells.

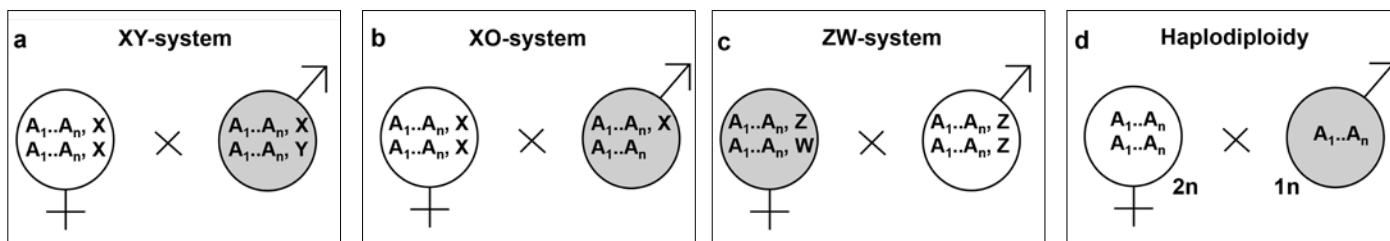
Haplodiploid species do not carry differentiated sex chromosomes but have both sexes differing in the number of copies of all chromosomes (figure 2d). Males are haploid, having one copy of each chromosome, and develop from unfertilised eggs. Females are diploid, carrying each chromosome in duplicate, and develop from fertilised eggs. All ants, bees, wasps and sawflies (Hymenoptera) and thrips (Thysanoptera) are haplodiploid (Beukeboom & Perrin 2014). Gynandromorphic individuals can be mosaics of haploid and diploid tissues, but can also be entirely haploid or diploid.

Gynandromorphism in haplodiploids

There are various developmental defects by which gynandromorphs can arise in haplodiploid organisms, some of which are similar to diplo-diploid species, but there are also haplodiploid-specific causes. Causes that are shared between both ploidy types are double fertilization or partial loss of the genetic information for sex determination, whereas ploidy level (complete chromosome set) differences are specific to haplodiploids. To distinguish between these causes requires information about the sex determination system and ploidy level of the individuals, information that is not always easily available.

1. Binucleation of the egg prior to fertilization

A common developmental aberration is that an egg starts dividing before it is fertilised by a sperm cell (figure 3a). Each nucleus in a binucleated egg may subsequently be fertilised by a separate sperm cell. In diploid individuals this can be an X-carrying and a Y-carrying sperm, resulting in an XX-XY mosaic that is partly female and partly male. Such individuals have for example been reported from the fly *Drosophila subobscura* Collin in Gordon, 1936 (Hollingsworth 1955), but also from a grasshopper (XX-XO mosaic, White 1968) and the silk moth *Bombyx mori* (Linnaeus, 1758) (ZZ-ZW mosaic, Goldschmidt & Katsuki 1927). In haplodiploid organisms, both nuclei may also be fertilised with a sperm cell with different genetic information for sex determination (see 1B), but in contrast to diploid organisms, it is also possible that one nucleus is fertilised and the other not.



2. Various forms of sex determination among insects. Diploid species (a-c) carry two copies of all regular chromosomes (called autosomes, indicated as A_1 to A_n) and a pair of sex chromosomes. Under male heterogamety (a-b), males have either two different sex chromosomes, an X and an Y (a) or only a single X chromosome (b), whereas females have two X chromosomes. Under female heterogamety (c), females carry two different sex chromosomes, a Z and a W, and males have two Z chromosomes. Under haplodiploidy (d), females carry all regular chromosomes in duplicate and are diploid ($2n$, where n stands for the number of different chromosomes), whereas males have a single copy of each chromosome and are haploid ($1n$). The number of regular chromosomes differs per species.

2. Verschillende vormen van geslachtsbepaling in insecten. Diploïde soorten (a-c) dragen twee kopieën van alle reguliere chromosomen (autosomen geheten, aangegeven als A_1 tot A_n) en één paar geslachtschromosomen. Onder mannelijke heterogamete (a-b), hebben mannetjes ofwel twee verschillende geslachtschromosomen, een X en een Y (a) of slechts één X chromosoom (b), terwijl vrouwtjes twee X chromosomen hebben. Onder vrouwelijke heterogamete (c), dragen vrouwtjes twee verschillende geslachtschromosomen, een Z en een W, en hebben mannetjes twee Z chromosomen. Onder haploïdie (d), dragen vrouwtjes alle reguliere chromosomen in duplo en zijn diploïd ($2n$, waarbij n het aantal verschillende chromosomen aangeeft), terwijl mannetjes één kopie van ieder chromosoom hebben en haploïd ($1n$) zijn. Het aantal reguliere chromosomen verschilt per soort.

1A. Binucleation of the egg followed by a single fertilization

In haplodiploids, this results in a mosaic individual with both diploid (female) and haploid (male) tissue. Such individuals can be recognised by flow cytometry, a method to measure DNA content of cells. They show both a haploid ($1n$) and a diploid ($2n$) peak on the flow cytometry readout (Beukeboom *et al.* 2007). Such individuals have for example been reported from the honeybee *Apis mellifera* Linnaeus, 1758 (Rothenbuhler *et al.* 1952).

1B. Binucleation of the egg followed by double fertilization

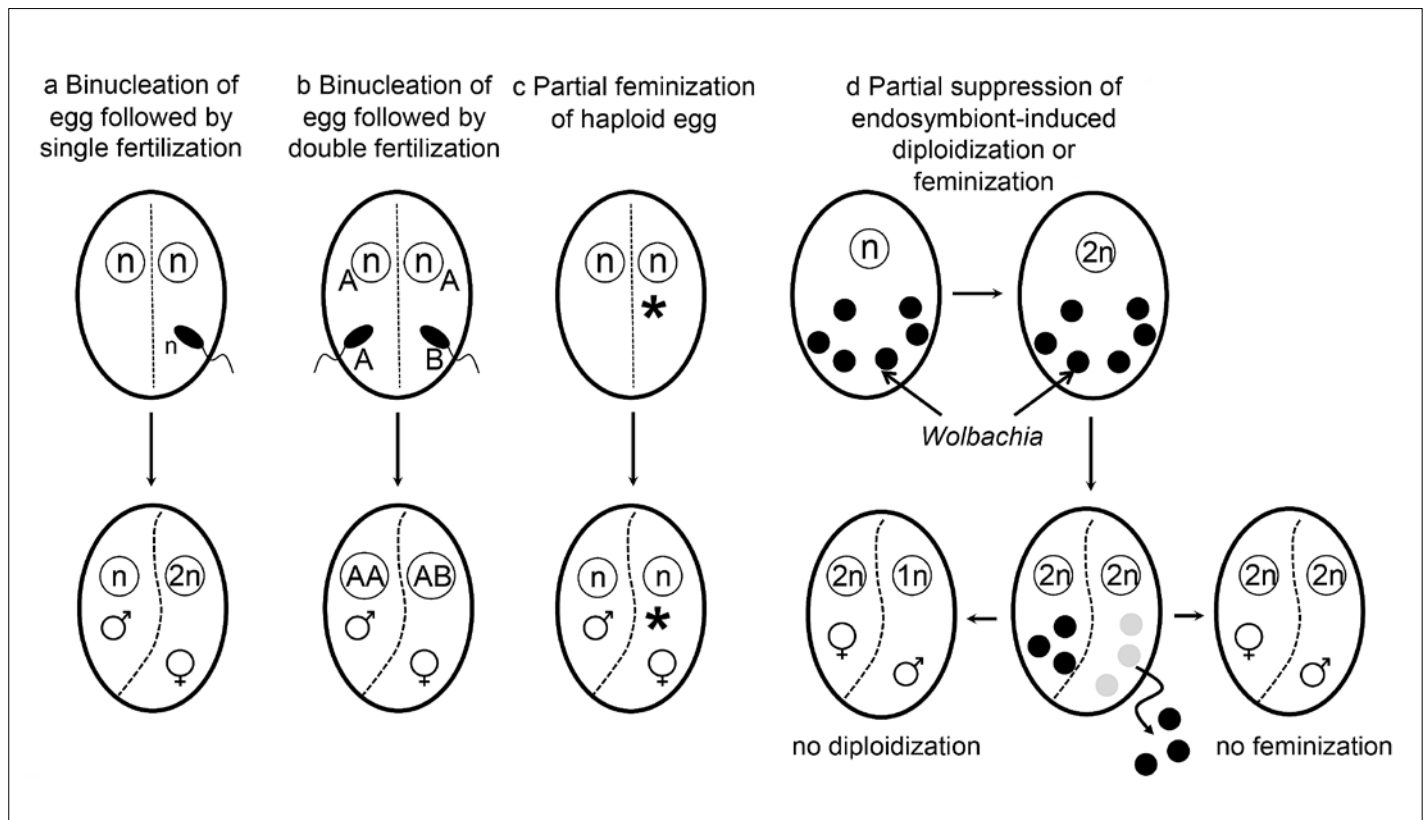
Double fertilization of a binucleated egg in haplodiploids will result in a mosaic individual with only diploid tissue. This may go unnoticed because the individual will be entirely diploid and female. However, there exists a sex determination mechanism among Hymenoptera that may cause an entirely diploid individual to develop as a sexual mosaic. This complementary sex determination system (figure 4) is predominantly present in ants, bees and several parasitoid taxa (Van Wilgenburg *et al.* 2006, Heimpel & de Boer 2008). Under complementary sex determination the sex of an individual is determined by alleles (protein products) of a specific sex determination gene. There typically exist many different alleles of this gene within a species. Two different alleles in a diploid individual together form a dimeric product that is needed for female development (Beye 2004). Haploid individuals carry only one allele and are always male, but diploid individuals with two identical alleles develop into diploid males. If one nucleus of a binucleate egg is fertilised by a sperm with an identical sex allele and the other is fertilised by a sperm with a dissimilar allele, a partial male and partial female diploid individual may develop. Although such double fertilization of a binucleate egg by a matching and a non-matching sperm is theoretically possible, no cases have yet been reported. One reason may be that it is hard to demonstrate and another that it would require a double mating, requiring sperm of two different males, because hymenopteran males are (normally) haploid and produce one type of sperm only. The gynandromorphic honeybee reported by Rothenbuhler *et al.* (1952) appears to be a haplo-diploid mosaic rather than the result of a double fertilization after binucleation of the egg.

2. Feminization of a haploid egg

Although haploid embryos typically develop into males in Hymenoptera, some exceptional haploid specimens have been reported. From the chalcidoid *Nasonia vitripennis* (Walker, 1836), gynandromorphs are known that are entirely haploid (Beukeboom *et al.* 2007). Their occurrence can be understood from *Nasonia*'s sex determination mechanism. *Nasonia* has a different sex determination gene than in the abovementioned complementary sex determination system. This sex determination gene needs to be active in an embryo to initiate female development (Verhulst *et al.* 2013). This is accomplished by the father who transmits an active copy of the gene via his sperm to a fertilised egg. The mother silences this gene during egg formation and transmits it in an inactive form to her eggs (Zou *et al.* 2020). This means that haploid embryos only have an inactive gene from the mother and become male, whereas diploid embryos from fertilised eggs have an inactive (from the mother) and an active (from the father) gene and develop into a female. The gynandromorphic individuals are believed to be the result of an aberrant female that is not able to entirely inactivate the sex determination gene in her eggs. This leads to a haploid individual in which some cells become female and others male (figure 3c). Conversely, it would also be possible that the activity of the father's gene copy is corrupted and this might lead to a diploid gynandromorphic individual, although this has not yet been reported. The *Nasonia* sex determination system has not yet been documented in any other hymenopteran, but it is expected to occur more widespread.

3. Partial suppression of endosymbiont-induced diploidization or feminization

Many hymenopteran species are thelytokous, they reproduce clonally and only have females that develop from unfertilised diploid eggs. A well-known example in the Ichneumonidae is the worldwide occurring diplazontine species *Diplazon laetatorius* (Fabricius, 1781). Thelytokous reproduction is often caused by infection with endosymbionts, such as the bacteria of the genera *Wolbachia* or *Cardinium* (Werren *et al.* 2008). Although females lay haploid eggs, the endosymbiont causes doubling of all chromosomes (diploidization) during the first egg division without forming two daughter cells (Cordaux *et al.* 2011). The result is a diploid embryo that develops into a female. Tulgetzke



3. Various causes of gynandromorphism in Hymenoptera. A premature division of an egg may result in a binucleate egg (a-c) of which either one (a) or both (b) nuclei can be fertilised. A single fertilization (a) leads to a haplodiploid mosaic gynandromorph, whereas a double fertilization (b) leads to a diploid mosaic that can develop into a gynandromorph if each nucleus is fertilised by a sperm that carries a different complementary sex determination allele (see text and figure 4). (c) A mutation in a sex determination gene (indicated with asterisk) can cause gynandromorphism through partial feminization of a haploid embryo leading to a haploid gynandromorph. Partial masculinization of a diploid embryo by mutation of a gene required for female development is also possible (not shown). (d) Endosymbionts in thelytokous species cause diploidization and feminization of unfertilised eggs. Gynandromorphism may result from loss of the endosymbiont in some cells, yielding haplodiploid mosaics (left option) or partially feminized individuals (right option). Figure adapted and extended from Narita et al. (2010).

3. Verschillende mogelijke oorzaken van gynandromorfie in Hymenoptera. Een voortijdige deling van een ei kan resulteren in een ei met twee kernen (a-b) waarvan ofwel één (a) ofwel beide (b) kernen bevrucht kunnen worden. Een enkelvoudige bevruchting (a) leidt tot een haplodiploïde mozaïeke gynandromorf, terwijl een dubbele bevruchting (b) tot een diploïde mozaïeke gynandromorf kan leiden als iedere kern wordt bevrucht door een spermacel die een ander complementair geslachtsbepalingsallel draagt (zie tekst en figuur 4). (c) Een mutatie in een geslachtsbepalingsgen (aangeduid met een sterretje) kan tot een haploïde gynandromorf leiden via gedeeltelijke feminisatie van een haploïde embryo (d). Endosymbionten in thelytoke soorten induceren diploidisatie en feminisatie van onbevruchte eieren. Gynandromorfie kan ontstaan door verlies van de endosymbiont in sommige cellen, resulterend in haplodiploïde mozaïeken (linker optie) of gedeeltelijk gefeminiseerde individuen (rechter optie). Figuur aangepast en uitgebreid van Narita et al. (2010).

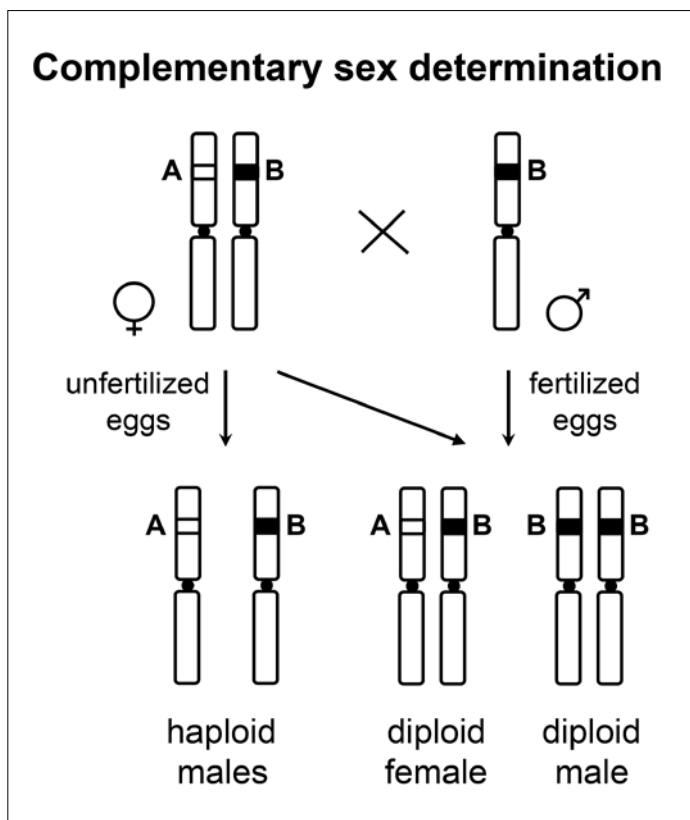
& Stouthamer (2012) reported that this process can partially fail in the chalcidoid *Trichogramma kaykai* Pinto & Stouthamer, 1997 resulting in gynandromorphic individuals. Cells in which the bacteria are lost do not diploidise and remain haploid, resulting in male tissue.

There are two complexities to this partial thelytokous development that are relevant to the origin of gynandromorphism. Giorgini et al. (2009) found that if the *Cardinium* endosymbiont is lost in the thelytokous chalcidoid *Encarsia hispida* De Santis, 1948, individuals still become diploid. These individuals are however male rather than female, indicating that the bacteria do not diploidise but only feminize the (diploid) embryos. If the endosymbiont would become lost in part of the cells of this species, the result would be a gynandromorph with diploid female as well as diploid male cells. Ma et al. (2015) reported that in the thelytokous braconid *Asobara japonica* Belokobylskij, 1998 diploidization and feminization occur as separate steps during development, each requiring a specific titre of the *Wolbachia* bacteria. At low bacterial titre neither diploidization nor feminization occurs, resulting in haploid males. At intermediate titre diploidization occurs but no feminization, leading to diploid males. A high

titre is needed to both diploidise and feminize the embryos to develop as females. Partial loss of the bacteria may thus have various effects, causing either haploid or diploid male tissue. Except for *Trichogramma*, cases of gynandromorphism based on partial loss of the endosymbiont in thelytokous species, are not known. It is currently also unclear how many thelytokous species adhere to the two-step mechanism of thelytoky as reported by Ma et al. (2015).

Mosaicism patterns

The distribution of male and female parts in gynandromorphs can vary. A bilateral (left-right) pattern is common, but may also be most easily observed, as it is manifested by several female characteristics on one side and several male characteristics on the other side of the body. Such individuals are, for example, very obvious in butterflies that have different morphology and colour of female and male wings. In contrast, gynandromorphs in hymenopterans often appear to have an anterior-posterior pattern, with female traits in the front and male traits in the back of the body. Why this anterior-posterior pattern is frequent in Hymenoptera remains unknown.



Conclusions

Gynandromorphic individuals occur occasionally in hymenoptera and other insects. They are the results of developmental errors. Multiple causes of gynandromorphism are known from haplodiploids. They require knowledge of the reproductive mode of the insect as well as its sex determination mechanism. Gynandromorphic individuals can in turn be informative about the underlying sex determination mechanism. It is often not easy to distinguish between the possible causes of gynandromorphism as it requires specific molecular techniques, such as destructive flow cytometry. The cause of gynandromorphism in the here reported *D. montanus* and *S. cognata* also remains unknown. The most likely explanation is that they resulted from a binucleate egg in which one nucleus was fertilised and the other not, as this appears to be the most common cause of gynandromorphism. Another argument is that complementary sex determination is known to occur in the Ichneumonidae.

Acknowledgements

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4. Complementary sex determination in Hymenoptera. The sex of an individual is determined by complementary alleles on a sex determination gene. Two different alleles in diploids result in female development, whereas a single allele in haploids leads to male development. A diploid egg with two identical alleles develops into a diploid male.
4. Complementaire geslachtsbepaling in Hymenoptera. Het geslacht van een individu wordt bepaald door complementaire allelen van een geslachtsbepalingsgen. Een set van twee verschillende allelen in diploïden resulteert in vrouwelijke ontwikkeling, terwijl een enkelvoudig allel in haploïden tot mannelijke ontwikkeling leidt. Een diploïd ei met twee gelijke allelen ontwikkelt zich tot een diploïd mannetje.

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Samenvatting

Hoe gynandromorfen ontstaan in Hymenoptera, met twee nieuwe vondsten voor de familie Ichneumonidae

De vondst van een gynandromorf van de ichneumonide *Dicaelotus montanus* (De Stefani, 1885) door Dick Belgers te Wageningen leidde tot een levendige uitwisseling van e-mails tussen beide auteurs over het ontstaan van gynandromorfie en tot dit artikel. Bij de gevonden *D. montanus* is sprake van een wesp met een vrouwelijke kop, inclusief de antennen, en een mannelijk achterlijf. De tweede auteur vond nog een tweede voor-achtergynandromorfe ichneumonide: *Sussaba cognata* (Holmgren, 1858). Hier is de kop grotendeels mannelijk en de rest van het lichaam vrouwelijk. Bij Hymenoptera is in het algemeen sprake van een haplo-diploïdsysteem van geslachtsbepaling: onbevuchte, haploïde, eieren leveren een mannetje en diploïde, bevuchte, eieren een vrouwtje. Gynandromorfen ontstaan doordat er in sommige lichaamscellen fouten optreden tijdens de ontwikkeling. Er worden een drietal mogelijkheden van dergelijke 'fouten' besproken: (1) Partiële celdeling van het ei waarbij een dubbele kern ontstaat zonder dat de cel in twee dochtercellen splitst, gevolgd door een enkele dan wel dubbele bevruchting. (2) Feminisatie van een haploïd ei dat normaliter tot een mannetje zou leiden. Dit is tot nu toe alleen bekend van de Pteromalide *Nasonia vitripennis*. (3) Partiële onderdrukking van symbiontgeïnduceerde diploïdisatie of feminisatie. In sommige soorten zijn er alleen vrouwtjes die zich parthenogenetisch voortplanten (thelytokie). In de eieren zijn bepaalde bacteriën aanwezig, zoals *Wolbachia* of *Cardinium* die ervoor zorgen dat de chromosomen set verdubbelt voordat de eerste eiceldeling plaatsvindt. Soms gaan de bacteriën verloren in een deel van de cellen en ontstaat er een gynandromorf. Dit is gevonden bij de chalcidoid *Trichogramma kaykai*. Bij de hier gepresenteerde gynandromorfen lijkt de meest waarschijnlijke oorzaak de onder (1) genoemde reden waarbij in sommige eicellen één kern is bevrucht en de andere niet. *Dicaelotus montanus* is nieuw voor de fauna van Nederland.



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