The Evolution of Alternative Genetic Systems in Insects

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Evolutionary transitions between genetic systems in insects.
The Major Genetic Systems of Insects...

- **Diplodiploidy** - Every male inherits one haploid genome from his mother and one haploid genome from his father, and these two haploid genomes have equal probability of transmission through his sperm.
  - All mammals, all birds and most other vertebrates

- **Haplodiploidy** - A male transmits only his mother’s genome.

- **Thelytoky** - A female transmits only her mother’s genome; no sons are produced, only daughters.
Diplodiploidy

- Every individual has two parents and carries a diploid genome consisting of one haploid genome from each parent.
Diplodiploidy

Every individual has two parents and carries a diploid genome consisting of one haploid genome from each parent.

This genetic system characterizes all mammals, birds, most vertebrates and a large majority of insects.
Haplodiploidy…

- A sex-determining mechanism found in some insect groups among which males are haploid and females are diploid
- Best known form: arrhenotokous haplodiploidy
  - Males develop from unfertilized eggs via apomixis
  - Females usually diplo-diploid
Arrhenotokous haplodiploidy is found in...

These are small, slender insects with *rasping-sucking mouthparts*. Wings, when present, are narrow and fringed with long *hairs*...

**Thysanoptera**

Unique characteristic: mouthparts where the mandibles and maxillae have evolved into a proboscis, sheathed within a modified labium to form a "beak"

**Hymenoptera**

**Coleoptera**

**Hemiptera**
Xyleborini and Dryocoetini

- Phloem-feeding bark beetles are associated with a complex microbiota of bacteria and fungi for which they act as vectors.
- Some species harbor transovarially transmitted endosymbiotic bacteria.
Hypothenemus hampei

- Only male-haploid beetle system known outside of arrhenotokous clade Xyleborini and Dryocoetini
- The Coffee berry borer
- One of the most serious pests of coffee
  - Endosulfan
  - Cephalonomia stephanoderis & Prorops nasuta (bethylids), Phymastichus coffea (Eulophid), and the braconid Heterospilus coffeicola
What do all of these insects have in common?
How did haplodiploidy come about?

- Arises in lineages that use woody plant stems as a food source, either wood or sap
  - Of the nine in our paper, 6 associated with dead wood, other 3 associated with phloem sap

- Why is this important?
  - Woody plant stems are a nutritionally poor resource, and insects that rely on them usually also rely on maternally inherited bacteria
Hamilton speculates…

- This could be the outcome of the conflict over sex determination between intracellular bacteria and their host.
  - Endosymbionts want to feminize their host → so host moves and multiplies the sex determining factors across the genome
  - Gives bacteria more targets for elimination, until all surviving autosomes behave like X chromosomes and sex determination relies on chromosome dosage.
Paternal Genome Elimination (PGE)...

- Males begin life as diploid zygotes but ultimately produce sperm that carries on their mothers genome
  - Also referred to as “male haploidy” or uniparental male systems”
Different mechanisms/timing of paternal genome elimination (PGE)

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- **Diaspidid**: Embryonic paternal genome elimination.

Herrick & Seger: Early (diaspidid) PGE should be derived due to escalating conflict between male and female genomes.

Different mechanisms/timing of paternal genome elimination (PGE)

- Lecanoid/Comstockiella: Gametic paternal genome elimination.
- Diaspidid: Embryonic paternal genome elimination.
- THIRD FORM OF PGE: PARTHENOGENESIS

Coccoidea
Sciaridae: dark-winged fungus gnats

Unique?
- The PGE system of sciarids is apparently unique in that the paternal autosomes are expressed in males, in contrast to the inactivation or early elimination of paternal autosomes in scale insects, Hypothenemus, and mites.
- Tendency to produce unisexual broods, either all male or all female.
  - What would be the benefit of an all male brood?
- It is unclear whether the fungi on which they depend are vectored by adult sciarids and thus potentially “inherited”
Other Genetic Systems...

- Hermaphroditism - an insect that has reproductive organs normally associated with both male and female sexes
- Only one genus of scale insect
  - *Icerya purchasi*
    - Have the ability to produce both eggs and sperm
    - Sperm inherited transovarially
    - Multigenerationally inherited
Thelytoky

- The genetic system is which females transmit only the maternal genome and produce ONLY daughters
- No mating occurs
  - Apomixis - eggs are produced mitotically
  - Automixis - eggs are produced via meiosis and are refused
- This system completely lacks males
Obligate Thelytoky

*Trichogramma* wasp

*Rose Gall Wasp*

*Broad-nosed Weevil*
Obligate Thelytoky: Conversion of Arrhenotokous Haplodiploidy to Thelytoky by Wolbachia
Conversion of Arrhenotokous Haplodiploidy to Thelytoky by *Wolbachia*

- Conversion of a lineage that produces males parthenogenetically to one in which females are produced parthenogenetically…
  by feminizing the sons

- This can be seen in the Rose Gall Wasp
Wolbachia-induced Thelytoky in the Rose Gallwasp

- Plantard et al. 1998 studies the reproductive systems of the rose gallwasp, *Diplolepis spinosissimae*, which exhibited two different reproductive systems.

- Of the ten populations studied, eight were thelyokous and males were extremely rare in these populations.
  - Can anyone guess what was different in these eight populations?
Wolbachia-induced Thelytoky in the Rose Gallwasp

- The obligate thelytoky was only found in the population infected with *Wolcachia*, the two other populations were not infected with the endosymbiont.

- They were able to determine that the thelytoky was a result of the Wolbachia because after antibiotic treatment the females were able to produce males.
Contagious Thelyoky

- Conversion of sexual populations into asexual ones via (1) genes causing asexuality in populations where gene flow still exists between asexuals and their sexual relatives or (2) Wolbachia-induced parthenogenesis.
Wolbachia-induced parthenogenesis

- The female lays her egg into an egg infected with Wolbachia
- Her uninfected egg becomes infected
- Within a few generations the progeny is entirely thelytokous

Trichogramma wasp
Hybridization and Thelytoky

• Believed that all origins of obligate thelytoky from obligate diplodiploidy involve hybridization

• This has occurred in the broad-nosed weevils (Normark 1996)

• A mitochondrial DNA study of the *Aramigus tessellatus* found 12 distinct maternal lineages
Cyclic Thelytoky

- Eight origins of cyclic thelytoky, 5 of them in insects
- Unmated females produce males
Cyclic Thelytokty
Aphids: Aphidoids

- Females are XX and males are XO
  - The elimination of the X chromosome in the males has recently been shown to be random with respect to parent of origin

- This is different from parental genome elimination because in PGE the males are diploid and during mitosis the genes acquired from the father are eliminated
Aphids

Fig. 1
Cyclic Thelytoky: Oak Gall Wasps

- The cyclic thelytoky in oak cynipids is unusual because the two reproductive modes alternate and there is only a single generation of each per year.

- Oak cynipids commonly complete a sexual-asexual cycle in a single year which means they are... bivoltine
Mixed Genetic System...

- When virgin females give birth to diploid males this can also be called arrhenotoky
  - Seen in Aphids
**Micromalthus debilis**

- Live in rotting wood
- Mostly find larviform females. Why?
- Give birth to live larvae, whom are young with legs called triungulin
- Triungulin molts into legless larva which could develop into…
  - A pupa that then merges as a winged adult
  - A larviform female that will itself will give birth to triungulins
  - A larviform female that lays a single male egg that hatched into a larva that eats its mother
  - A larviform female that can reproduce in both of the latter ways.
El Fin...