

THE EVOLUTION OF ALTERNATIVE GENETIC SYSTEMS IN INSECTS

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■ **Abstract** There are three major classes of insect genetic systems: those with diploid males (diplodiploidy), those with effectively haploid males (haplodiploidy), and those without males (thelytoky). Mixed systems, involving cyclic or facultative switching between thelytoky and either of the other systems, also occur. I present a classification of the genetic systems of insects and estimate the number of evolutionary transitions between them that have occurred. Obligate thelytoky has arisen from each of the other systems, and there is evidence that over 900 such origins have occurred. The number of origins of facultative thelytoky and the number of reversions from obligate thelytoky to facultative and cyclic thelytoky are difficult to estimate. The other transitions are few in number: five origins of cyclic thelytoky, eight origins of obligate haplodiploidy (including paternal genome elimination), the strange case of *Micromalthus*, and the two reversions from haplodiploidy to diplodiploidy in scale insects. Available evidence tends to support W.D. Hamilton's hypothesis that maternally transmitted endosymbionts have been involved in the origins of haplodiploidy. Bizarre systems of extrazygotic inheritance in Sternorrhyncha are not easily accommodated into any existing classification of genetic systems.

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INTRODUCTION

The laws of genetics are not universal: They vary from species to species. The adaptive significance of this variation is poorly understood and constitutes a central problem in evolutionary biology (3, 64, 69, 82, 113). A staggering range of different genetic systems is found within insects, and the purpose of this review is to survey this diversity and to characterize the broad pattern of its evolution. I do not review the ecological patterns of the distribution of parthenogenesis or the hypotheses for the adaptive significance of sexuality, both of which have received thorough attention elsewhere (7, 53, 80). I briefly review the major classes of genetic systems and then discuss the patterns of evolutionary transition between them, giving case histories for the rarest transitions. Finally, I discuss strange patterns of extrazygotic inheritance that do not fit into existing classifications. Throughout, I highlight recent progress as well as outstanding problems that remain.

THE MAJOR GENETIC SYSTEMS OF INSECTS

A classification of the major genetic systems of insects is presented in the Appendix. It is useful to recognize three basic classes of systems: those with diploid males, those with effectively haploid males, and those without males. I refer to

these as diplodiploidy, haplodiploidy, and thelytoky (see Appendix, below). There are also mixed systems that can be seen as straddling the boundaries between these three basic classes (Figure 1).

Hermaphroditism

Before discussing the diversity of genetic systems that occur in insects, I must acknowledge one class of systems that is conspicuous by its absence: hermaphroditism. Although extremely important in the multicellular biota in general (35), hermaphroditism (monoecy) is almost unknown in insects. It has been reported from one genus of scale insects (see Additional Paternal Genomes, below). Otherwise, apart from occasional developmental anomalies, insects appear to be obligately gonochoristic (dioecious), with individuals differentiating either as males or as females. This apparent constraint on the evolution of insect genetic systems, in spite of the high frequency of hermaphroditism in close insect relatives such as Crustacea (77), is one of many unexplained phenomena in this field of inquiry.

Diplodiploidy

Diplodiploidy, or amphimixis with diploid males (Appendix, I.A), needs little introduction. It characterizes all mammals, all birds, most other vertebrates, and a large majority of insect species. Diplodiploidy is the most thoroughly sexual class of genetic systems, in that the complete cycle of meiosis and syngamy occurs in each generation. Every individual has two parents and carries a diploid genome consisting of one haploid genome from each parent. Each parent contributes to each offspring a recombined haploid genome in which maternally derived and paternally derived chromosome regions have equal probabilities of being represented. This review of "alternative genetic systems" focuses on those systems that lack diploid males, so little more will be said about diplodiploidy. However, many of the evolutionary dynamics of alternative genetic systems depend on features of the diplodiploid systems from which they arise (27, 149), and the interplay between the details of diplodiploid systems (especially sex-determining mechanisms and extent of intersexual conflict) and the evolutionary dynamics of alternative systems arising from them is likely to be a fruitful area of future research.

Thelytoky

In this review I use the term thelytoky in the broad sense to refer to genetic systems in which females transmit only maternal genes and produce only daughters. Thus, it encompasses systems that completely lack males as well as the rarer systems in which mating with males of a related species is necessary to initiate development. This category of genetic systems is ill served by existing terminology. The most popular term for these genetic systems is parthenogenesis, but the etymology of this term (virgin birth) has encouraged scholars to apply it as well to arrhenotoky (virgin birth of males) and deny its application to sperm-dependent systems. Clonality is another candidate term, but it does not really apply to automictic systems

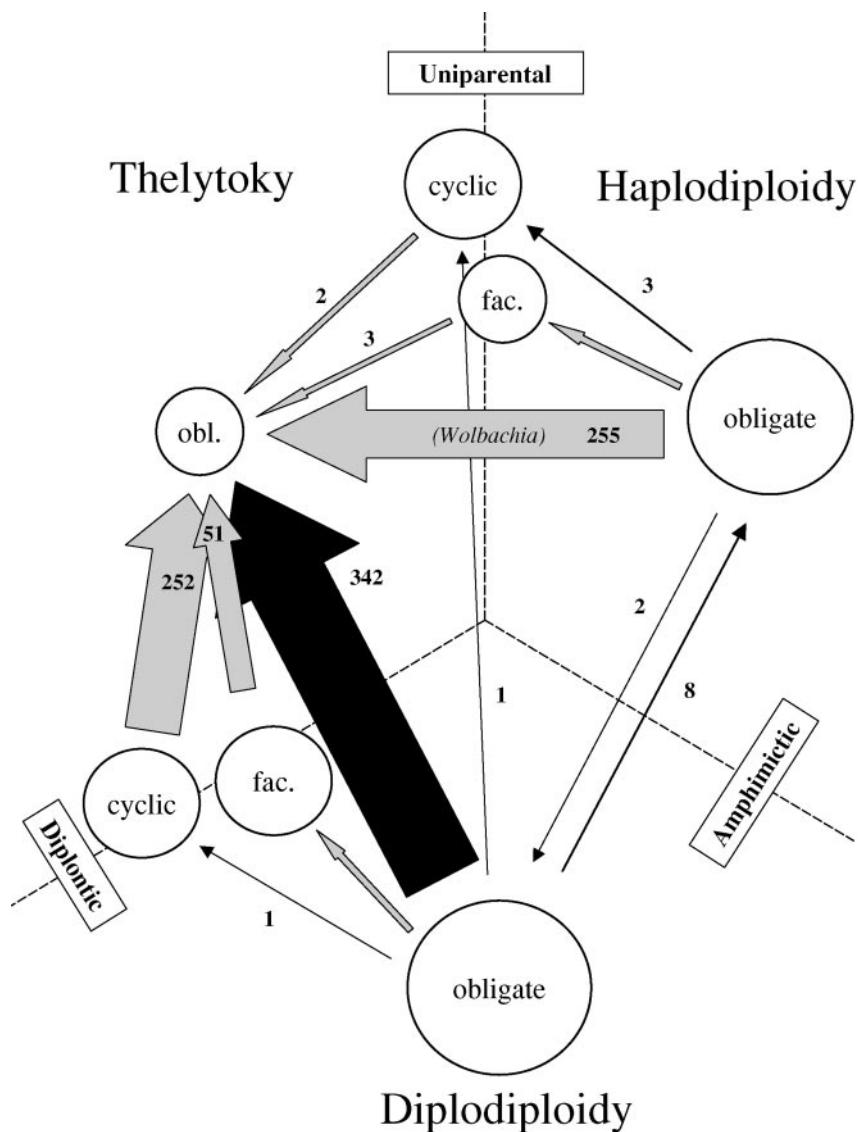


Figure 1 Evolutionary transitions between genetic systems in insects. Mixed systems, cyclic and facultative (fac.), are drawn at the boundaries between the systems they alternate between. For definitions, see the Appendix. The *gray block arrows* represent transitions that are relatively likely to be reversible. The other *arrows* represent transitions for which reversal is relatively rare or unlikely. The *circles* are drawn with diameters roughly proportional to the logarithm of the estimated total species diversity of lineages having that genetic system. To estimate the number of transitions to obligate (obl.) thelytoky, I compiled a database of over 900 insect species in which the existence of at least one obligately thelytokous lineage has been reported or can be inferred. A list of these species and bibliographic references is available as Supplemental Material: Follow the Supplemental Material link on the Annual Reviews homepage at <http://www.annualreviews.org/>. The other transitions are discussed in the text.

(Appendix, II.A.2) in which recombination occurs. The term thelytoky has the disadvantage of being unfamiliar to most biologists, but it may be gaining currency because of its widespread use in the burgeoning literature on *Wolbachia*, intracellular bacteria that often convert one form of parthenogenesis into another when they convert arrhenotokous haplodiploidy (Appendix I.B.1) to thelytoky.

The major features of thelytoky are (a) reproductive efficiency, with little or no energy wasted on “all this silly rigamarole of sex” (61), and (b) a lack of recombination between the genomes of different individuals. Thelytoky occurs frequently in many groups of organisms but is especially frequent in small invertebrates inhabiting freshwater and terrestrial environments (7, 33, 78, 134), and the large number of thelytokous insect lineages reflects this pattern.

Haplodiploidy

The best-known form of haplodiploidy is arrhenotokous haplodiploidy, in which males develop from unfertilized eggs (Appendix, I.B.1). This system is often called simply arrhenotoky, meaning virgin birth of males. But virgin females give birth to diploid males in some mixed genetic systems such as that of aphids, and this is also called arrhenotoky (14). In addition to arrhenotokous haplodiploidy, there is another class of genetic systems in which males begin life as diploid zygotes but ultimately produce sperm that carry only their mother’s genome (Appendix, I.B.2). Here I refer to these as systems of paternal genome elimination (PGE) (67). PGE is identical to arrhenotokous haplodiploidy in terms of transmission genetics. Other authors have referred collectively to all systems with haplodiploid transmission genetics as “male haploidy” (26) or “uniparental male systems” (27), but here I use the term haplodiploidy in this broad sense to cover all such systems. Previously the term haplodiploidy has been used in the entomological literature as a simple synonym for arrhenotokous haplodiploidy and in the acarological literature to refer collectively to those systems in which males have a haploid soma (41, 110), arrhenotokous haplodiploidy, and embryonic PGE (Appendix, I.B.2.a).

Mixed Systems

This is an extremely heterogeneous category of genetic systems, covering all those complex systems in which there is an alternation (either facultatively or cyclically) between two of the different genetic systems described above. No system of alternation between diplodiploidy and haplodiploidy has ever been described, even though diploid males can occur at high frequencies in otherwise haplodiploid populations (119) and can be fertile (83). Rather, it is always thelytoky that alternates with one of the other systems.

A simplified classification of mixed genetic systems is presented in the Appendix, focusing on whether thelytoky alternates with diplodiploidy or haplodiploidy, and whether the alternation is cyclic or facultative. Because these mixed systems embody transitions between genetic systems, they are potentially a rich source of insights into the evolutionary history of such transitions. There have been relatively few origins of cyclic thelytoky. An excellent review of these has

been published (66), to which I add some updated information below. Facultative thelytoky presents a more difficult problem, in part because it is more difficult to detect. A classification of modes of facultative thelytoky and an attempt to identify the evolutionary origins of facultative thelytoky in insects would be most valuable and is beyond the scope of this review.

MAJOR PATTERNS IN THE EVOLUTION OF INSECT GENETIC SYSTEMS

The apparent patterns of transition between genetic systems in insects are summarized in Figure 1. This figure relies on estimates of quantities that are in many cases poorly known. The overwhelming trend apparent from the figure is that the most frequent genetic-system transitions seen in insects are transitions to obligate all-female systems from each of the other (partially or wholly amphimictic) systems. Although virtually every student of genetic systems has been convinced of the reality of this trend (7, 71, 100, 134), many details are difficult to establish.

The gray arrows in Figure 1 indicate transitions that are likely to be relatively easily reversible. The transitions from mixed systems (the cyclically and facultatively amphimictic systems arrayed along the dotted border lines) to obligate parthenogenesis are expected to be reversible (at least early in their evolutionary history) because mixed systems are all capable of some kind of reversion to amphimixis following one or more parthenogenetic generations. For instance, a temperate aphid lineage transported to the tropics may become obligately apomictic (Appendix, II.A.1) in the absence of a photoperiodic cue to switch to amphimixis, but descendants reinvading the temperate zone may readily recover a sexual phase. Transitions from arrhenotokous haplodiploidy to obligate thelytoky are also expected to be subject to reversal because in the ancestral arrhenotokous system a virgin female is capable of producing males and this capacity may in principle be switched back on. In the case of *Wolbachia*-induced thelytoky, this reversal has been effected experimentally in many cases (22, 148). Of course, not all the transitions encompassed by the gray arrows are reversible. There are several cases of *Wolbachia*-associated thelytoky in which 'curing' the *Wolbachia* infection leads to sterility but not to a reversal to arrhenotokous haplodiploidy (22). And there are also several aphid species in which extensive experimental efforts have failed to elicit a switch to a sexual phase (59, 126).

The large black arrow in Figure 1 represents the largest class of genetic-system transitions, from obligate diploidy to obligate thelytoky, and indicates that these are relatively unlikely to revert to amphimixis. For instance, the majority of these transitions occur in weevils, in which the obligately all-female lineage is typically triploid or has an even higher ploidy level, which makes meiosis extremely problematic. Also, these weevils are derived from lineages in which the males had Y chromosomes, chromosomes that do not occur in females and are therefore extinct. Of course it might be possible to recapture a Y chromosome from a related

species or otherwise reinvent the male, but the obstacles to reversion are generally much higher in these cases than in those indicated by the gray arrows (28, 107).

ORIGINS OF OBLIGATE THELYTOKY

The standard model of the evolution of obligately thelytokous lineages holds that they arise more or less frequently from amphimictic populations and may be briefly favored by selection, but that, on an evolutionary timescale, they quickly go extinct. This pattern is reflected in Figure 1. In spite of the large number of thelytokous insect lineages and their importance in the historical discovery of parthenogenesis (7, 101, 141), in recent years other groups such as vertebrates and aquatic invertebrates have been more prominent in studies of obligate thelytoky (2, 34, 46, 50, 78, 140). But there are a few areas in which a good deal of progress has been made lately, and some of these are discussed below.

Conversion of Arrhenotokous Haplodiploidy to Thelytoky by *Wolbachia*

Fields of scientific inquiry undergo periodic revolutions, precipitated by new theoretical frameworks or new technologies. It is much rarer for a field to be revolutionized by the discovery of a simple, long-overlooked fact. But this is what has happened to the study of insect genetic systems following the 1990 discovery that experimental applications of antibiotics can convert thelytokous wasp lineages back to arrhenotokous haplodiploidy (133). By 2000, nearly one half of all new journal articles on alternative insect genetic systems were devoted to the effects of *Wolbachia* or other microbial agents, and this proportion shows no signs of declining. I do not dwell on this copious new literature because it has been amply reviewed elsewhere (22, 36, 148).

The fervor for *Wolbachia* studies is justified, as their advent represents an unusual forward leap, both theoretically and empirically, for the study of insect genetic systems. Note, however, that microbial agents have been found to induce only 1 of the 20 types of genetic-system transitions diagrammed in Figure 1: the transition from obligate haplodiploidy (specifically arrhenotoky) to obligate thelytoky. And, indeed, the expression parthenogenesis-inducing or parthenogenesis induction in reference to *Wolbachia* is misleading because there are no established cases of a nonparthenogenetic lineage rendered parthenogenetic by *Wolbachia*. What *Wolbachia* does in these cases is convert a lineage in which males are produced parthenogenetically to one in which females are produced parthenogenetically, by feminizing (through genome doubling) parthenogenetically produced sons.

It is possible that *Wolbachia* or other maternally inherited elements are involved in other genetic-system transitions as well, but such involvement has yet to be clearly demonstrated. In the case of transitions from mixed haplodiploid-thelytokous systems to obligate thelytoky, studies have found no evidence for *Wolbachia* involvement (132, 147). Possibly, mixed genetic systems are more likely

to be robust to manipulation by *Wolbachia* because (a) selection on maternal elements to induce obligate thelytoky is weaker in a mixed system than in an obligately sexual system (a mixed system realizes some of the twofold fitness advantage of thelytoky, so selection to induce further thelytoky is less than twofold), and (b) mixed systems must have specific adaptations for the recovery of the sexual phase of the life cycle.

Probably the best candidate for another genetic-system transition induced by microbes is the most frequent transition observed: the origin of obligate thelytoky from obligate diplodiploidy (Figure 1). There is evidence that *Wolbachia* plays a role in the origins of parthenogenesis in weevils (104, 131, 148). However, in this case, and perhaps more generally for ancestrally diplodiploid lineages, there is little scope for a role of *Wolbachia* in maintaining thelytoky. *Wolbachia*-infected parthenogenetic weevils are polyploid, and male weevils typically have a Y chromosome (128). Thus, there is little chance that administration of antibiotics (to XXX females) will result in viable male (XY) offspring. Understanding the historical role of *Wolbachia* in the origin of such diplodiploid-derived parthenogenetic lineages is an area for future research.

Contagious Thelytoky

Classically, origins of thelytoky have been modeled as independent spontaneous mutations arising within sexual populations. Recently, two cases have been described in which sexual populations acquire thelytoky from preexisting conspecific thelytokous lineages. One of these involves *Wolbachia*. The phylogenetic incongruence between *Wolbachia* and their hosts has widely been interpreted as indicating frequent horizontal transfer of *Wolbachia* between widely disparate groups of insects (150). Experimental transfers have typically resulted in unstable, symptom-free infections (22). But in *Trichogramma kaykai*, an egg parasite, uninfected larvae sharing an egg with *Wolbachia*-infected conspecifics readily become infected, and within a few generations their progeny can be entirely thelytokous (70).

A different mechanism for the transfer of obligate thelytoky has recently been described in aphids as a second form of contagious parthenogenesis (126). Some aphid lineages that never produce sexual females do produce some males, which can apparently introduce genes for obligate thelytoky into otherwise sexual (cyclic diplodiploid-thelytokous) populations. Similar mechanisms for the spread of thelytoky have long been thought to occur in other cyclically parthenogenetic and hermaphroditic taxa, but only recently has there been evidence that it occurs in an insect, the aphid *Rhopalosiphum padi* (47).

Hybridization and Thelytoky

Our understanding of the role of hybridization in the origin of obligately thelytokous insect lineages has lagged far behind our understanding of the same question in vertebrates. Virtually all thelytokous vertebrates are of hybrid origin (2). In insects,

Wolbachia-induced thelytoky has nothing to do with hybridization (22, 148), and neither do most losses of the sexual phase in aphids (14, 59, 126). Nonetheless, it is possible that most or all origins of obligate thelytoky from obligate diplodiploidy (the only type of transition seen in vertebrates) do involve hybridization, although we know frustratingly little about this topic, with information available for only a few species. In a pioneering 1978 study, Drosopoulos (48) synthesized a hybrid triploid pseudogamous leafhopper lineage in the laboratory. The majority of transitions from obligate diplodiploidy to obligate thelytoky occur in broad-nosed weevils (Curculionidae: Entimini) (97), and there is good evidence of hybrid origin of one weevil species (131, 137).

Hybridization is also clearly involved in at least some cases of transition from facultative diplodiploidy-thelytoky to obligate thelytoky, as has been demonstrated for two species in the stick insect genus *Bacillus* (91). Several lines of evidence have demonstrated the hybrid ancestry of the apomictic species *Bacillus whitei* and *B. lynceorum*. Studies of *Bacillus* have also resulted in the first discovery of hybridogenesis (previously known only in vertebrates) in insects, as well as the discovery of androgenesis, which is the formation of new individuals by the fusion of two sperm (92, 136).

Hybridization with sexual lineages may also be involved in the subsequent evolution of obligately thelytokous lineages (89, 123). Genes from sexual lineages may introgress into obligately thelytokous lineages (8), or occasionally genes from obligately thelytokous lineages may introgress into sexual populations, as in the bizarre case of androgenesis (91, 136).

Genome Evolution

We still do not understand the major consequences of the loss of sex for the evolution of eukaryote genomes. For instance, it has not yet been possible to determine whether deleterious mutations are continually accumulating in the genomes of thelytokous lineages, as implied by some theories of sex (80, 108), or how transposable elements typically respond to the loss of sex (1).

Diploidy, the presence of exactly two copies of each autosome and each of its constituent loci, is a necessary feature of some stage of every sexual life cycle. In the mechanics of the cell cycle, diploidy is both an artifact of syngamy and an adaptation for meiosis. The origin of obligate apomixis coincides with a loss of the cytogenetic constraint to remain diploid. A nondiploid structure has long been known for the karyotypes of some obligately apomictic aphid lineages (11, 12), and the karyotypes of apomictic aphids can evolve rapidly (105, 129, 151). The diploid structure of the ribosomal DNA array is typically lost early in the history of apomictic lineages of aphids (15) and may also be lost in stick insects (94), although in both thelytokous aphids and stick insects the evolution of rDNA arrays can be complex (19, 94). Comparative studies of other repetitive sequences in both groups are ongoing (16–18, 90, 93, 95, 124, 130).

Persistence of Obligately Thelytokous Lineages

Although most obligately thelytokous lineages are apparently of recent origin (64, 100), in the past few years there has been considerable interest in the possibility of identifying “ancient asexuals” (78, 87, 96). Until recently, it had been thought that the highest-ranking (and thus potentially most ancient) strictly thelytokous taxon of insects was the aphid tribe *Tramini* (59, 126, 145). However, the recent discovery of sexual *Tramini* has shown this to be incorrect (13).

None of the most ancient asexuals (tens of millions of years old) are insects (78). However, if “ancient” is defined as more than one million years (My) old (87), then there are a number of candidates. The nonhybrid automictic stick insect species *Bacillus atticus* may have diverged from its closest sexual relative about 15 My ago (91), and thelytokous lineages within the stick insect genus *Timema* may be more than 1 My old (87, 122). For one thelytokous weevil lineage, an age of 2 My has been estimated (104), although possibly with some history of introgression from sexual lineages (107). In aphids, the thelytokous species *Tuberolachnus salignus* shows hints of an accumulation of deleterious mutations, possibly as a consequence of long-term thelytoky (108). Even within the aphid species *Rhopalosiphum padi*, some clones appear to be hundreds of thousands of years old (47, 125).

ORIGINS OF CYCLIC THELYTOKY

In contrast to the origins of obligate thelytoky (which are many) and the origins of facultative thelytoky (which are hard to assess), the origins of cyclic thelytoky are relatively few and well defined. Of the eight origins of cyclic thelytoky in animals, five occurred in insects. Here I briefly discuss each of these, focusing on improvements in phylogenetic resolution that have occurred since the excellent review by Hebert (66). Cyclic thelytoky requires unmated females to produce males, which places severe constraints on the sex determination system (66) and helps explain the apparent association between haplodiploidy and cyclic thelytoky evident in Figure 1.

Aphids

The single origin of cyclic alternation between thelytoky and diploidy occurred in the branch leading to all extant Aphidoidea (Phylloxeridae, Adelgidae, and Aphididae), sister group of the Coccoidea (scale insects). Aphidoidea thus account for the entire pathway in Figure 1 connecting this system to others, and hence for 3 of the 20 types of genetic-system transitions seen in insects. Apomictically produced aphid females with XX sex chromosome karyotypes produce XO males by eliminating one X chromosome. In contrast to the PGE displayed by some other cyclically thelytokous insects (sciarids and possibly cecidomyiids) and by close relatives of aphids (most scale insects), the elimination of the X chromosome has recently been shown to be random with respect to parent of origin (152).

Micromalthus debilis

Micromalthus debilis is typically paedogenetic, consisting entirely of thelytokous larviform females (112). Under poor culture conditions, haploid male and diploid female imagoes are produced. The origin of *M. debilis* is depicted with the longest arrow in Figure 1, crossing the center of the diagram. *M. debilis* is a single species that is not closely related to anything else; recent evidence suggests that it is a basal lineage within Archostemata, the basal-most suborder of beetles (9). Every other extant lineage in that region of insect phylogeny is obligately diploid; however, it seems likely that the lineage leading to *M. debilis* must have passed through a period of obligate haplodiploidy before arriving at the complex system seen today (in which case Figure 1 would show nine origins of obligate haplodiploidy and four transitions from obligate haplodiploidy to cyclic haplodiploidy-thelytoky).

Oak and Maple Gall Wasps

Cyclic thelytoky characterizes a clade within the gall wasps (Cynipidae) consisting of the two tribes Cynipini (oak gall wasps) and Pediaspidini (maple gall wasps) (115, 132). This is the only group of metazoans in which there is obligate alternation between thelytokous and amphimictic generations (66). Stone et al. (132) provide an excellent recent review of their biology.

Heteropezini

Heteropezini is a tribe of cecidomyiid midges within the subfamily Porricondylinae (51). Its most likely sister group is the tribe Winnertziini (45, 155). Like *Micromalthus*, they are paedogenetic, with thelytokous generations becoming reproductively mature at a subadult stage. This stage varies between species, some reproducing as larvae and others as pupae (155). The developmental mechanisms of paedogenesis in *Heteropeza* have recently been studied by Hodin & Riddiford (68).

Mycophila + *Tekomyia*

Cyclic, paedogenetic thelytoky has arisen in a second group of cecidomyiid midges (51), in the tribe Aprionini (72, 74) within the subfamily Lestremiini (73). The developmental mechanism of paedogenesis in *Mycophila* is substantially different from that in *Heteropeza* (68).

THE ORIGINS OF HAPLODIPLOIDY

A great deal of importance has been placed on the ecological context in which obligate thelytoky tends to arise (7, 53, 141); indeed, the ecological constraints on the distribution of thelytokous lineages has received considerably more theoretical and empirical attention than the cytogenetic constraints on their origins (7, 29). In the case of haplodiploid lineages, the opposite is true. A number of authors have considered the genetic and cytogenetic constraints on origins of haplodiploidy

(21, 27, 56, 127), but their ecological distribution has received less attention for several good reasons. Thelytokous lineages are many and recent, providing abundant evidence of the ecological situations in which they tend to arise. Their relative cytogenetic simplicity and wide phylogenetic scatter imply relatively few constraints on their origins. Haplodiploid lineages, in contrast, are few and ancient. The ecological circumstances of their origins are often obscure, and the unlikelihood of evolving viable haploid males would seem to be severe.

And yet, if one does investigate the ecological circumstances in which haplodiploidy tends to arise, a fairly clear pattern emerges. In insects, haplodiploidy arises in lineages that use woody plant stems as a food source, either wood or sap. W.D. Hamilton (62) noted the tendency for haplodiploidy to arise in insects that live under the bark of dead trees: Of the nine origins in insects, discussed below, six probably occurred in association with dead wood. The other three origins occurred in insects that feed on phloem sap. Hamilton (63) also noted another common feature of these lineages that might shed light on the origins of haplodiploidy: Woody plant stems are a nutritionally poor resource, and insects that rely on them usually also rely on maternally inherited bacteria.

The nature of the connection between maternally transmitted bacteria and haplodiploidy is unclear. Hamilton speculated that haplodiploidy might be the final outcome of a history of conflict over sex determination between intracellular bacteria and their hosts. In Hamilton's scenario, endosymbionts seek to feminize their hosts by attacking and eliminating male-determining sex chromosomes; hosts respond by moving and multiplying the sex-determining elements across the genome. This in turn gives the bacteria more targets for elimination, until finally all the surviving autosomes behave like X chromosomes and sex determination rests on chromosome dosage alone.

Micromalthus debilis

Micromalthus debilis, whose phylogenetic affinities and life cycle are discussed above, feeds on rotting wood, as do most of its relatives in Archostemata. In all stages of the life cycle, gram-positive bacteria are abundant in the fat body and hemolymph. Their maternal transmission is indicated by their presence in ovarioles and developing eggs (85).

Xyleborini and Relatives

Arrhenotokous lineages in the scolytine beetle tribes Xyleborini and Dryocoetini have recently been shown to represent one large haplodiploid clade, with over 1000 species (75, 76, 106). The transition to haplodiploidy occurred in a phloem-feeding lineage. Many 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 (25, 109). There is some experimental evidence that at least one of the arrhenotokous species is unable to reproduce when treated with antibiotics (109).

Hypothenemus and Relatives

Outside of the arrhenotokous clade discussed above, there is just one species of bark beetles (Coleoptera: Curculionidae: Scolytinae) in which a male-haploid system has been demonstrated. This is the species *Hypothenemus hampei*, the coffee berry borer, in which a system of germline PGE (Appendix) was recently reported (24). However, this species is nested within what appears to be a much larger clade of inbreeding species, and it is likely that male haploidy is common to all of them. This putative clade contains about 190 species and consists of the genera *Hypothenemus*, *Cryptocarenum*, *Trischidias*, and *Periocryphalus* (79). The sister group of this clade is unknown. It is traditionally placed in the tribe Cryphalini, but recent molecular studies have cast doubt on the monophyly of Cryphalini without producing strong support for any alternative grouping (49). Like many bark beetles (including *Coccotrypes*), *H. hampei* has transovarially transmitted bacteria concentrated in the Malpighian tubules (25).

Sciaridae

Sciarid fungus gnats have a system of germline PGE (67). The term genomic imprinting was originally coined to describe chromosome behavior in *Sciara* (88). The PGE system of sciarids is apparently unique in that the paternal autosomes are expressed (or at least not heterochromatinized) in males, in contrast to the inactivation or early elimination of paternal autosomes in scale insects, *Hypothenemus*, and mites. Among the many other unusual features of sciarid genetic systems is a tendency to produce unisexual broods, either all male or all female (114). Some sciarids are commercially important as pests in mushroom houses (65), and there are ongoing empirical and theoretical (57, 121) studies of their genetics (4, 10, 102) and cytology (20). The ancestral ecology of Sciaridae is probably feeding on fungi in association with rotting wood (99). Intracellular bacteria are not known from Sciaridae (25), and it is unclear whether the fungi on which they depend are vectored by adult sciarids and thus potentially “inherited.”

Hymenoptera

The order Hymenoptera is the most species-rich haplodiploid clade. The vast majority of hymenopteran species are strictly arrhenotokous. Although the Hymenoptera have diversified into a vast array of ecological niches and are best known as parasitoids, predators, and nectar-feeders, the larvae of most of the basal lineages of Hymenoptera (sawflies) feed on dead wood (116, 142) and harbor intracellular maternally inherited bacteria (25). Hymenoptera arose early in the history of the Holometabola (84). The larval habit of feeding in rotting wood may be primitive in Holometabola, and arrhenotokous haplodiploidy in both Hymenoptera and *Micromalthus* may be a legacy of the ancestral holometabolan habitat (62).

Thysanoptera

The thrips, like the Hymenoptera, comprise a primitively arrhenotokous order (66a). Feeding on fungi associated with dead wood appears to be the primitive habit in Thysanoptera, exemplified by the extant lineage Merothripidae (103a). Some fungus-feeding thrips have been thought to harbor maternally transmitted bacterial endosymbionts (25), but this may be an error (139a).

Aleyrodidae

Whiteflies comprise an arrhenotokous family within the hemipteran suborder Sternorrhyncha. The most likely sister group of the Aleyrodoidea is Coccoidea (scale insects) + Aphidoidea (aphids) (32, 144). Virtually all Sternorrhyncha feed on phloem sap and rely on maternally inherited bacterial endosymbionts in specialized organs termed bacteriomes or mycetomes (5), and there have been numerous recent studies of the phylogeny and physiology of whitefly endosymbionts (31, 38, 39, 103, 135).

Iceryini

Iceryini is an arrhenotokous tribe of scale insects (111) (Sternorrhyncha: Coccoidea). The phylogenetic position of Iceryini within the otherwise diplodiploid family Margarodidae is not well resolved (55). Some of iceryines are androdioecious, consisting of hermaphroditic individuals and males (54, 111, 120), a system otherwise unknown in insects and rare in arthropods (146). Like most Sternorrhyncha, iceryines harbor maternally transmitted intracellular bacteria. Among the tribes of the family Margarodidae, there is a great diversity of bacteriome configurations and modes of transmission (25). Little is known about these, except what Buchner discovered in a series of beautiful histological studies in the 1960s (138).

Most Neococcoidea

Most of the extant species of scale insects (Sternorrhyncha: Coccoidea) have a system of PGE. The basal families of scale insects (Margarodidae, Ortheziidae, Phenacoleachiidae, Putoidae) are primitively diplodiploid, but the majority of scale insect families (and a large majority of species) comprise a monophyletic clade characterized by PGE (37). Strikingly similar habits and morphology are conserved across the origin of the PGE clade, making possible a fairly clear picture of the ancestral situation in which PGE arose. The sister group of the PGE clade is the family Putoidae, and the basal lineage of the PGE clade is the family Pseudococcidae. Both putoids and pseudococcids are “mealybugs” and have only recently been recognized as separate families. Both harbor bacteriome-associated, maternally transmitted, intracellular bacteria. The bacterial endosymbionts of pseudococcids have recently been found to include the only known example of a bacterium endosymbiotic within another bacterium (143). Little is known of the endosymbionts of putoids.

There appears to be some evolutionary instability in the PGE system of scale insects. Embryonic PGE has evolved from germline PGE repeatedly within the family Diaspididae (67). More strikingly, the only two known cases of reversion from haplodiploidy back to diplodiploidy have been found in scale insects, in the genera *Stictococcus* and *Lachnodius* (37, 111). *Stictococcus* has an unusual system of sex determination in which embryos that receive bacteria develop as females and those that do not develop as males (25), supporting Hamilton's conjecture of a role for endosymbionts in the evolution of haplodiploidy. *Stictococcus* is also unusual in that embryos are nourished via a placenta, tissue derived from the embryo that digests the maternal nurse cells (25). This coincidence between the loss of PGE and the gain of a placenta in the evolutionary lineage leading to *Stictococcus* tends to cast doubt on Haig's (56, 58) contention that there is no adaptive connection between the genomic imprinting seen in paternal genome-eliminating insects and the genomic imprinting seen in placental mammals and plants.

Other Probable Cases

CECIDOMYIIDAE A diversity of complex chromosome cycles is found in cecidomyiid midges (Diptera). One common feature of these is that one set of chromosomes is eliminated during spermatogenesis (23), as in Sciaridae. It seems likely that it is the paternal genome that is eliminated, as in Sciaridae and other chromosome-elimination systems, but this has never been clearly demonstrated in Cecidomyiidae (23, 27). Chromosome elimination had been suggested as a synapomorphy uniting a monophyletic Sciaridae + Cecidomyiidae (153), but a more-thorough analysis has indicated that these are not sister taxa but instead represent independent origins of unusual genetic systems (98) in a similar ecological situation (99). A similar case of possibly paternal chromosome elimination has recently been found, slightly outside the Insecta proper, in the collembolan suborder Symphypleona (43, 44).

FOUR SMALL CLADES OF SCOLYTINE BEETLES Extreme inbreeding (regular brother-sister mating) has frequently evolved in association with haplodiploidy (60, 154). Of the clades discussed above, four (Hymenoptera, Thysanoptera, and the two bark beetle clades) include extreme inbreeders. Hamilton (60) described a set of characteristics correlated with extreme inbreeding and haplodiploidy, including extremely female-biased sex ratios and small flightless males. He predicted that taxa with this suite of characters would turn out to be haplodiploid, and where this prediction has been tested it has turned out to be correct (24, 40). According to Hamilton's criteria we can predict that haplodiploidy will be found in four additional clades within the beetle subfamily Scolytinae (Curculionidae): throughout the genera *Premnobius* (106) and *Sueus* and within the genera *Araptus* and *Bothrosternus* (79).

EXTRAZYGOTIC INHERITANCE

It is a general feature of metazoan life cycles that they contain a single-celled zygote stage. Even in vegetative reproduction, mediated by many-celled propagules, there is still an occasional passage through a single-celled zygote (30). This fact is implicit in classifications of metazoan genetic systems, such as that in the Appendix, which essentially are classifications of modes of zygote production (81).

However, there are some insect genetic systems that, remarkably, lack a one-celled zygote stage and in which new individuals are founded by two genetically different lineages of cells or of nuclei. Such developmental modes do not fit neatly into any classification of modes of zygote production. Here I classify these according to whether they have additional paternal genomes (in the form of sperm pronuclei, even when these are inherited from the mother) or an additional maternal genome (in the form of maternal polar bodies or cell lineages derived from the mother). These unusual developmental modes are found only in the hemipteran suborder Sternorrhyncha.

Additional Paternal Genomes

Iceryine scale insects have been classified as hermaphrodites because unmated, anatomically female individuals contain active sperm that fertilize their eggs to produce diploid female progeny. Careful study of *Icerya purchasi* by Royer (120) revealed that multiple sperm pronuclei are transovarially transmitted from mothers to daughters and that they autonomously proliferate in the bodies of the daughters and migrate into the next generation of eggs. Hermaphroditism may be an inadequate term to describe this situation. It could alternatively be characterized as involving "totipotent sperm" or "a permanent cancer of the germline." *I. purchasi* is primarily selfing. However, if there is occasional outcrossing, then there will be competition between the indigenous lineages of sperm pronuclei (those inherited from an individual's parent) and the newly introduced lineages (those received from its mate) for representation in the offspring and in future generations. The fact that this remarkable system characterizes a widespread economic pest (*I. purchasi* is the cottony-cushion scale) raises hope for the practicability of its further study.

Additional Maternal Genomes

Sometimes the transmission of endosymbionts from mother to offspring in the Sternorrhyncha is accompanied by the transmission of entire cells from the maternal bacteriome. This process has been studied recently in whiteflies (39, 135), in which maternal bacteriocytes eventually break down and release their endosymbiotic bacteria (25, 135). The putoid mealybugs, sister group to the large PGE clade of scale insects, also transmit intact bacteriocytes from mother to offspring. However, in the case of the putoids, these maternal bacteriocytes never break down

and release their endosymbionts. They proliferate to form the bacteriome of the offspring and persist from generation to generation (25).

Intriguingly, the shift from diplodiploidy to haplodiploidy in scale insects seems to have coincided with a revolution in the mode of formation of the bacteriome. The formation of the bacteriome in the haplodiploid (PGE) pseudococcid mealybugs is different from that in the diplodiploid putoids, but it still involves the inheritance of additional maternal genomes. In typical metazoan oogenesis, meiosis occurs and results in one haploid egg nucleus and three additional haploid genomes in the form of polar bodies. Typically, the polar bodies degenerate. But in Pseudococcidae, the polar bodies do not degenerate. They migrate into the developing embryo and (sometimes following fusion with a cleavage nucleus from the embryo) proliferate to form the embryo's bacteriome (139). This is the only case in nature of maternal polar bodies forming a permanent part of the soma of their offspring. The closest parallel may be the role of polar bodies in the angiosperm seed, which is also (like the bacteriome) involved in nutrition, but which (in contrast to the bacteriome) is active only for a short time early in the ontogeny of the offspring and is never fully integrated with it physiologically.

If a placenta is an outgrowth of an embryo that invades the body of its mother, then the bacteriome of Pseudococcidae might be termed an antiplacenta, an outgrowth of a mother that invades the body of its offspring. Thus, the origin of haplodiploidy in scale insects is coincident with the origin of an antiplacenta. Recall that in the scale insect genus *Stictococcus*, there is a reversal in the direction of flow of tissues and gene products, with the origin of a normal placenta. And recall that this coincides with the reversion of haplodiploidy back to diplodiploidy. Possibly, mother-offspring interactions can help explain the differential fate of paternal versus maternal genes in paternal genome-eliminating insects, as they have in the case of genomic imprinting in mammals and angiosperms (58).

PROSPECTS

Insects have long played a critical role in furthering our understanding of the diversity of genetic systems and their evolution, from the first demonstration of parthenogenesis in aphids by Bonnet (134) to the recent elucidation of intragenomic conflict by Hamilton (60) and his followers (149). The adaptive significance of the laws of genetics remains a huge unsolved problem, which insects will no doubt be instrumental in helping us solve. In addition to the usual advantages of rearability and manipulability that have made model systems of the likes of *Drosophila*, insects have additional advantages that to date have been underexploited. One of these is the enormous diversity of insect genetic systems, whose faint outlines have been traced in this review. Another is the affinity between some of these truly strange animals and our agricultural ecosystems.

The low diversity and frequent disturbance of agricultural systems seems conducive to a number of clonal pests (6, 7, 86). There is a remarkable congruence

between the theoretical question of what makes clones vulnerable to extinction and the practical questions of how to precipitate extinctions of clonal pests while preserving the vitality of increasingly clonal crops. A number of agricultural systems are characterized by genetic system variation on three trophic levels. Consider an armored scale insect species such as *Aspidiotus nerii*, the oleander scale. It consists of sexual and clonal lineages (52), attacks a mosaic of sexual and clonal *Citrus* and other tree species, and is attacked by sexual and clonal *Aphytis* and other (often *Wolbachia*-infected) parasitic wasps (22, 117, 118). It will likely be from systems such as this, offering the possibility of switching Mendel's laws on and off in the various players in an ecosystem, that we will ultimately learn what Mendel's laws are for.

APPENDIX: CLASSIFICATION OF THE MAJOR GENETIC SYSTEMS OF INSECTS

A somewhat more detailed classification, with additional taxonomic information and references, is available via the Supplemental Material link on the Annual Reviews homepage at <http://www.annualreviews.org/>. The most important references are (7, 27, 66, 67, 134).

- I. **Obligate amphimixis** (sex, sexuality). Every female inherits one haploid genome from her mother and one haploid genome from her father.
 - (A) **Diplodiploidy** (diploid-male systems). 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. Found in large majority of all insect species; ancestral system in all orders except Thysanoptera and Hemiptera.
 - (B) **Haplodiploidy** (haploid-male systems, male haploidy, uniparental-male systems). A male transmits only his mother's genome.
 - (1) **Arrhenotokous haplodiploidy** (Arrhenotoky). Every male develops from an unfertilized egg and has only a haploid genome inherited from his mother. Found in Thysanoptera, Hymenoptera, Hemiptera, and Coleoptera.
 - (2) **Paternal genome elimination** [(PGE), paternal genome loss]. Every male develops from a zygote containing one haploid genome from his mother and one haploid genome from his father, but only the maternal genome is transmitted through his sperm. Found in Hemiptera, Coleoptera, and Diptera.
- II. **Thelytoky** (all-female systems, uniparental reproduction, parthenogenesis). A female transmits only her mother's genome; no sons are produced, only daughters.
 - (A) **Thelytokous parthenogenesis**. No mating occurs. There are no males.

- (1) **Apomixis** (ameiotic parthenogenesis, strict clonality). Eggs are produced mitotically. Found in several orders.
 - (2) **Automixis** (meiotic parthenogenesis). Meiosis occurs, but ploidy of eggs is restored through any of various mechanisms. Found in several orders.
- (B) **Sperm-dependent thelytoky** (obligate mating). Mating (with males of a related amphimictic population) is necessary to initiate development.
- (1) **Pseudogamy** (gynogenesis). Sperm activate development but the sperm nucleus does not fuse with the egg nucleus. Only maternal genes are transmitted to offspring (all daughters).
 - (a) **Apomictic pseudogamy**. Known in Hemiptera.
 - (b) **Automictic pseudogamy**. Known in Coleoptera and Lepidoptera.
 - (2) **Hybridogenesis** (hemiclonal inheritance). Syngamy occurs and the paternal genome is present and active in some of offspring (all daughters) but is eliminated during oogenesis. Known in Phasmatodea.
- III. Mixed systems.** Regular or irregular alternation between different genetic systems, typically between amphimixis and thelytoky.
- (A) **Thelytoky (or polyembryony) alternating with haplodiploidy.**
- (1) **Cyclic alternation.**
 - (a) **Polyembryony**. Clonal proliferation of embryos (male or female) by fission. Found in Hymenoptera.
 - (b) **Cyclic haplodiploidy-thelytoky** (cyclic parthenogenesis). Found in Hymenoptera, Coleoptera, and Diptera.
 - (2) **Facultative haplodiploidy-thelytoky** (facultative parthenogenesis). Any system in which reproduction may be either amphimictic or thelytokous. In most of these systems, reproduction is typically amphimictic, but unmated females may produce some viable offspring by thelytoky. Found in Hymenoptera and Hemiptera.
- (B) **Thelytoky alternating with diplodiploidy**
- (1) **Cyclic diplodiploidy-thelytoky** (cyclic parthenogenesis). Found in Hemiptera.
 - (2) **Facultative diplodiploidy-thelytoky** (facultative parthenogenesis). Found in several orders.

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