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Gynandromorphs and intersexes: potential to understand the mechanism of sex determination in arthropods

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Summary

Arthropods are sexually dimorphic. An arthropod individual usually differentiates into a male or a female. With very low frequencies, however, individuals with both male and female morphological characters have repeatedly been found in natural and laboratory populations of arthropods. Gynandromorphs (i.e., sexual mosaics) are genetically chimeric individuals consisting of male and female tissues. On the other hand, intersexes are genetically uniform (i.e., complete male, complete female or intermediate in every tissue) but all or some parts of their tissues have either a sexual phenotype opposite to their genetic sex or an intermediate sexual phenotype. Possible developmental processes (e.g., double fertilization of a binucleate egg, loss of a sex chromosome or upregulation/downregulation of sex-determining genes) and causal factors (e.g., mutations, genetic incompatibilities, temperatures or endosymbionts) for the generation of gynandromorphs and intersexes are reviewed and discussed.

Keywords

Arthropod; gynandromorph; insect; intersex; sex determination; sexual mosaic

Introduction

Unlike in plants and some groups of animals, hermaphroditism is extremely rare in arthropods (but see Hughes-Schrader and Monahan, 1966, for the exceptional case of coccids). In other words, an arthropod individual differentiates into a complete male or a complete female and does not become an intermediate, i.e., arthropods are sexually dimorphic. However, developmental defects, which occur at low frequencies under natural conditions, can lead to morphologically anomalous individuals with both male and female traits. Owing to their strangeness and rarity, such individuals often

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attract amateur insect collectors, and indeed, some of them are sold at surprising prices (e.g., the website Insect-Sale).

To date, numerous papers have reported the occurrence of arthropod individuals presenting phenotypically male and female parts. The distribution patterns of the male and female parts in such individuals are variable. For example, the male and female parts can be clearly bilateral, patchily distributed or uniformly mixed. Individuals with clear borders between the male and female parts are often referred to as gynandromorphs while those with ambiguous or no borders are usually referred to as intersexes. Although this classification based only on the external morphologies is quite common, it does not reflect the genetic and developmental processes. The biological definition of a gynandromorph (synonymous with a sexual mosaic) is a genetically chimeric individual while that of an intersex is a genetically uniform individual (e.g., Goldschmidt, 1934; Laugé, 1985), which will be explained in the following sections.

In this paper, we review (1) the occurrences of gynandromorphs and intersexes in arthropods, (2) the mechanisms of arthropod sex determination and (3) the possible developmental processes for the generation of gynandromorphs and intersexes. Finally, we discuss the significance of sexually anomalous individuals for better understanding the still unexplored sex-determining systems of arthropods.

Occurrence of male and female traits in a single individual

The occurrence of individuals consisting of phenotypically male and female parts has been reported repeatedly in arthropods. They have been found in both natural and laboratory populations of almost all orders of insects as well as non-insects (see Table 1). In many cases, however, it remains to be clarified whether they are gynandromorphs or intersexes and they are arbitrarily called gynandromorphs or intersexes. Considering the underlying processes, clearly bilateral individuals are likely to be gynandromorphs (see below for details).

We should exercise caution regarding the point that heterogeneous individuals are more likely to be detected in species in which the sexes are strikingly dimorphic than species in which the sexes are less strikingly dimorphic. Consequently, estimating the frequencies of occurrence merely through publication records can be misleading. Moreover, owing to their conspicuous features, the occurrence of clearly bilateral gynandromorphs may be published more frequently than the occurrence of ambiguous forms of gynandromorphs and intersexes.

To discriminate gynandromorphs and intersexes, it is necessary to identify the respective sexual genotypes of the tissues presenting male and female phenotypes. In species for which molecular analyses are unavailable, conventional karyotyping is widely used for sexual genotyping. In lepidopteran insects with a ZW-ZZ sex chromosome constitution, simple observation of the sex chromatin allows us to discriminate the male (ZZ) and female (ZW) genotypes. Sex chromatin is a highly condensed W chromosome that is visible in interphase nuclei (Traut and Marec, 1996). In insects for which molecular data are available, diagnostic polymerase chain reaction amplifications using Y-specific or W-specific molecular markers also allow us to discriminate the male and female genotypes. In addition, transcriptional analyses of genes expressed in sex-specific manners may also be used to confirm the male and female phenotypes in a single individual.

Sex-determining systems of arthropods

In the majority of insects, sex is genetically determined. For example, dipteran insects like the fruit fly *Drosophila melanogaster* have a male-heterogametic sex chromosome constitution (i.e., XX: female; XY: male). Lepidopteran insects like the silkworm *Bombyx mori* have a female-heterogametic chromosomal constitution (i.e., ZZ: male; ZW: female). Hymenopteran insects like the honeybee *Apis mellifera* have a haplodiploid sex determination system, in which fertilized (2n) eggs become females and unfertilized (n) eggs develop into males (Bull, 1983; Werren and Beukeboom, 1998; Heimpel and de Boer, 2008). The molecular mechanisms underlying sex determination and differentiation in the model insect *D. melanogaster* are well understood. At a very early embryonic stage, each cell determines its sex independently, and once determined, the sex of each cell is maintained during later development through a gene expression cascade consisting of *Sex-lethal* (*Sxl*), *transformer* (*tra*), *doublesex* (*dsx*) and other genes, in which sex-specific mRNA splicing plays an important role (Schutt and Nöthiger, 2000).

Although the molecular mechanisms of sex determination in non-*Drosophila* systems are not well understood, all the sex-determining mechanisms in insects are proposed to be variations of a single model consisting of a master regulator gene (like *Sex-lethal* in *D. melanogaster*) at the top of the cascade and the highly conserved *doublesex* gene at the bottom of the cascade (Figure 1) (Nöthiger and Steinmann-Zwicky, 1985; Hoy, 2003). Sex determination in a cell-autonomous manner is also believed to be widespread among insects on the basis that sexually mosaic individuals often occur in a diverse array of insects (Laugé, 1985).

Like insects, some of the non-insect arthropods are also considered to have genetically based sex determination. However, they differ from insects as sexual differentiation is deeply affected by sex hormones that are secreted by particular organs (e.g., the androgenic gland in crustaceans). It is known that some crustaceans are subject to environmental sex determination. In the shrimp *Gammarus duebeni*, sex is determined post-conception in response to photoperiod cues and is then fixed for life (Legrand et al., 1987).

Gynandromorphs

Gynandromorphs are chimeric individuals consisting of genetically male and genetically female tissues. In each cell of a gynandromorph, the genetic sex (e.g., sex chromosome constitution) is consistent with the sexual phenotype. In other words, the sex-specific expression or alternative splicing of sex-determining genes should be consistent with the genetic sex (Figure 2a). Gynandromorphs allow us to carry out fate mapping, which reveals the developmental history of each cell in the body of an

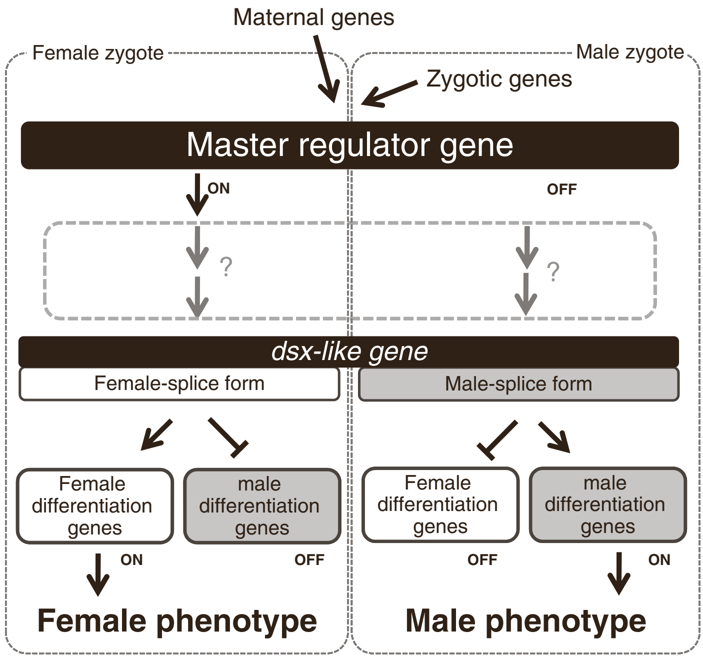

Figure 1. A proposed general model of sex determination in insects. This model assumes that the actions of both maternal genes and zygotic genes affect the expression of a master regulator gene, which corresponds to *Sex-lethal* in *D. melanogaster*. The expression of the master regulator gene activates or suppresses the expression of subsequent genes (downstream genes). At the end of the hierarchical gene expression cascade, a highly conserved *doublesex*-like gene is subjected to alternative RNA splicing and produces the male-specific protein DSX^M or female-specific protein DSX^F. The sex-specific DSX proteins activate and suppress a series of sex-specific differentiation genes, leading to either the female phenotype or the male phenotype.

organism (Garcia-Bellido and Merriam, 1969; Hotta and Benzer, 1972; Mori and Perondini, 1984; Milne and Rothenburler, 1983a; Myohara, 1994). The underlying causes of the generation of gynandromorphs are described below.

Gynandromorphs generated by loss or damage of a sex chromosome

In some insects like *D. melanogaster*, the number of X chromosomes (or Z chromosomes) relative to the number of autosomes is the initial key factor for sex determination. Loss of one of the X chromosomes during mitosis results in individuals with XX and X0 cells (Figure 3a). If the loss occurs during the first mitotic division (cleavage), individuals with 50% male tissues and 50% female tissues appear. Furthermore, the later the X chromosome is lost, the smaller the male part in the gynandromorph will be. In *D. melanogaster*, a mutant strain with an unstable ring-X chromosome often produces gynandromorphs (Hinton, 1955). In this strain, an X chromosome is easily lost during early cleavage, resulting in the frequent appearance of individual that are gynandromorphic at various degrees. The generation of gynandromorphs owing to loss

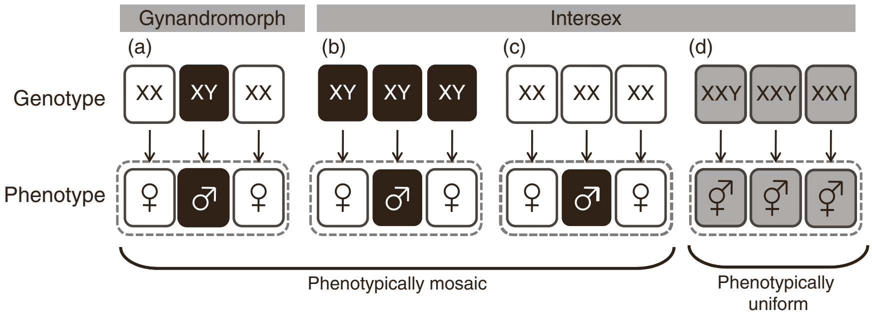

Figure 2. Relationships between the genotype and the phenotype of individual cells in gynandromorphs and intersexes. The squares indicate single cells (maleness: black; femaleness: white; intermediate: gray). The dotted lines indicate single individuals. For simplicity, a single individual is assumed to be composed of three cells. The genotype and phenotype are connected by arrows. (a) A gynandromorph (i.e., a sexual mosaic). (b) An intersex caused by partial feminization of a genetic male. (c) An intersex caused by partial masculinization of a genetic female. (d) An intersex with an intermediate genotype between male and female (e.g., a triploid intersex is shown).

of an X chromosome has also been reported in the fly *Sciara ocellaris* (Mori and Perondini, 1980).

Gynandromorphs generated from binucleate eggs

Double fertilization of a binucleate egg by X and Y sperms can also give rise to a gynandromorph in *Drosophila* (Hollingsworth, 1955). In lepidopteran insects such as *B. mori*, double fertilization of a binucleate egg (ZW) by Z sperms is thought to be the major cause of the generation of gynandromorphs (Goldschmidt and Katsuki, 1927). Since the female karyotype of *B. mori* is ZW, the meiotic division separates Z and W chromosomes, so that one remains in the egg and the other is discarded with the polar body. If the polar body is accidentally retained in the egg, both nuclei can be fertilized by Z sperms, resulting in the development of an individual that has male (ZZ) and female (ZW) tissues (Figure 3b). In some strains of *B. mori*, the polar bodies are prone to being retained in the eggs, leading to a high frequency of gynandromorphs (Goldschmidt and Katsuki, 1931). In the hymenopteran insect *A. mellifera*, fertilized eggs (2n) become females and unfertilized eggs (n) develop into males (Bull, 1983; Werren and Beukeboom, 1998). Accidental production of binucleate eggs (2n) followed by fertilization of one of the nuclei can result in the development of an individual that has male (n) and female (2n) tissues (Figure 3c).

Gynandromorphs generated by symbionts

Bacteria belonging to the genus *Wolbachia* (alpha subdivision of the phylum Proteobacteria) are ubiquitous endosymbionts of insects. In some hymenopteran insects, *Wolbachia*-infected females produce unfertilized eggs that parthenogenetically develop as females. Both antibiotic curing and high temperatures result in male production with elimination of the bacteria (Legner, 1985; Stouthamer and Luck,

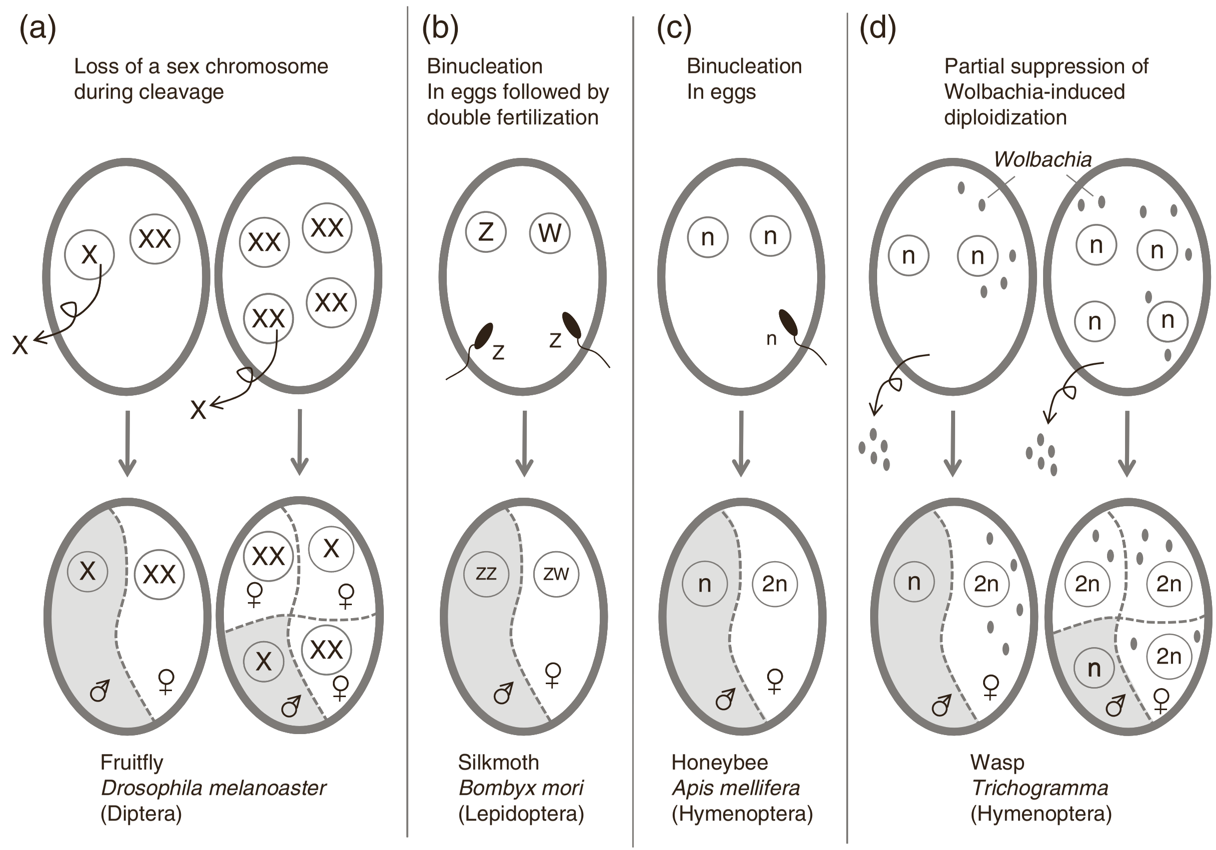

Figure 3. Possible examples of the developmental processes of gynandromorphs. (a) Loss of an X chromosome during mitosis in *Drosophila melanogaster*. (b) Double fertilization of a binucleate egg in *Bombyx mori*. (c) Fertilization of one of the nuclei in a binucleate egg in haplodiploid insects such as *Apis mellifera*. (d) Partial suppression of *Wolbachia*-induced diploidization during mitosis after antibiotic or heat treatments in haplodiploid wasps such as *Trichogramma* species. See the text for details.

1991; Zchori-Fein et al., 1992). Treatment with temperatures slightly higher than normal temperatures can give rise to gynandromorphs at high frequencies (Wilson and Woolcock, 1960; Bowen and Stern, 1966; Cabello and Vargas, 1985).

The cytogenetic mechanisms of *Wolbachia*-induced parthenogenesis have been studied in *Trichogramma* spp. and *Muscidifurax uniraptor* (Stouthamer and Kazmer, 1994; Legner, 1985). Meiosis is normal. In the first mitotic division, the chromosomes condense properly in prophase but fail to segregate in metaphase, resulting in diploidization of the nucleus and homozygosity at all loci.

It is considered that slightly high temperatures incompletely suppress the effects of *Wolbachia*. Under such conditions, diploidization may occur during the second cleavage or a later cleavage instead of the first cleavage and some nuclei escape diploidization and remain haploid (Figure 3d) (Stouthamer, 1997).

Intersexes

In contrast to gynandromorphs, intersexes are genetically uniform (Figure 2b-d). Some intersexes are genetically intermediate between the typical male genotype and the typical female genotype (e.g., XXY) and the sex-determining genes in every cell follow their own genetic signal (e.g., X:A ratio in *Drosophila*) (Figure 2d). On the other hand, other intersexes are genetically purely male or female, but some parts of their bodies have a sexual phenotype that is opposite to their genetic sex, i.e., partial feminization (Figure 2b) or partial masculinization (Figure 2c). However, all intersexes should be caused by defects in the processes of sex determination and differentiation, and thus strict classification of intersexes is of little importance. Here, we arbitrarily classify the intersexes according to the causal factors.

Intersexes generated by chromosomal aberrations

Genetic intersexes are individuals that are genetically intermediate between male and female. Triploid intersexes are one such example. In *Drosophila*, the initial signal for sex determination is the ratio of the X chromosome number to the autosome (A) number, in which XX;AA individuals (X/A = 1) become female and XY;AA individuals (X/A = 0.5) become male. In a triploid intersex (XXY;AAA) with an X/A ratio of 0.66, each cell differentiates into an intermediate sexual phenotype (Figure 2d). Triploid intersexes are also known in the moth *Solenobia triquetrella* (Seiler et al., 1958). Other types of intersexes are genetically purely male or female and some parts of their bodies are feminized or masculinized during the processes of sex determination and/or differentiation.

Intersexes generated by loss-of-function mutations

In *D. melanogaster*, loss-of-function mutations such as *Sex-lethal* (*Sxl*), *transformer* (*tra*), *intersex* (*ix*) and *doublesex* (*dsx*) exhibit sex reversal in their phenotypes. These are examples of phenotypic intersexes. Epistatic interactions between these mutations revealed by classical genetic experiments have allowed understanding the hierarchical gene expression cascade controlling sex determination in *Drosophila* (Schutt and Nöthiger, 2000). Furthermore, molecular genetic experiments have revealed that sex-specific mRNA splicing of the *Sxl*, *tra* and *dsx* genes plays a crucial role for sex determination in *Drosophila* (Schutt and Nöthiger, 2000).

Intersexes generated by crosses between different strains

In the moth *Lymantria dispar*, crosses between different geographic strains result in the generation of intersexes that exhibit a uniformly intermediate phenotype (Goldschmidt, 1934; Mosbacher, 1973). Since the karyotype of these individuals shows the female genotype (ZW), the cause of the intersexual phenotype is considered to be incomplete masculinization of genetic females. Likewise, hybridization between the closely related moths *Smerinthus ocellata* and *Smerinthus populi* results in the generation of intersexual offspring (Morgan, 1909). A particular genetic combination may affect the normal expression of the sex-determining genes in *L. dispar* and the *Smerinthus* species. The generation of intersexes through crosses between different strains or between closely related species may result from diverging sex-determining systems. It is generally considered that the sex-determining systems of arthropods are evolving rapidly (Werren and Beukeboom, 1998).

Intersexes generated by epigenetic factors

Environment

Exposure to high temperatures can induce partial feminization of genetic males in the mosquito *Culex stimulans* (Brust, 1966, 1968; Brust and Horsfall, 1965; Horsfall et al., 1964; Horsfall and Anderson, 1961, 1965; Craig, 1965). On the other hand, high temperatures induce masculinization in the bagworm *S. triquetrella* (Seiler, 1935) and stick insect *Carausius morosus* (Bergerard, 1958, 1961). Upregulation or downregulation of sex-determining genes induced by unusual temperatures may be possible causes of intersexual development. In the shrimp *G. duebeni*, photoperiods after mating determine the sex of the offspring (Legrand et al., 1987).

Sex hormone

In the firefly *Lampyris noctiluca*, transplantation of the larval male gonad into female larvae was reported to result in masculinization, suggesting the presence of a sex hormone in these insects (Naisse, 1966a, 1966b). This is an exceptional case among insects as sex hormones are generally considered to be absent. However, similar experiments carried out recently did not alter the sexual phenotype of these insects (Maas and Dorn, 2005). Therefore, the authenticity of hormone-associated masculinization in these insects and its relationship with the sex-determining genes remain unclear.

Symbionts

In some amphipods such as *G. duebeni* and *Orchestia gammarellus*, in which sex is determined environmentally, males can be partially or completely feminized by unicellular eukaryotes such as the microsporidian parasites *Octosporea effeminans* and *Nosema granulosis*, and the haplosporidian parasite *Paramartelia orchestiae*, leading to intersexual development (Bulnheim and Vavra, 1968; Bulnheim, 1977, 1978; Kelly et al., 2004; Ginsburger-Vogel, et al., 1980). In some isopods such as *Armadillidium vulgare*, sex is genetically determined but genetic males are known to be completely feminized by the endosymbiotic bacteria *Wolbachia* (Figure 2b) (Rigaud et al., 1997). In *A. vulgare*, heat treatment attenuates the effects of *Wolbachia* and leads to the generation of intersexes (Juchault et al., 1980). On the other hand, a virus is known to maculinize some of the tissues of *A. vulgare* genetic females, leading to the formation of intersexes (Figure 2c) (Juchault et al., 1991).

Wolbachia also have a feminizing ability of insect hosts. In the butterfly *Eurema mandarina* (former name *Eurema hecabe*, yellow-type), genetic males are completely feminized by *Wolbachia*. Antibiotic treatment of *E. mandarina* infected with feminizing *Wolbachia* results in the generation of intersexes (Narita et al., 2007a). On the other hand, in the moths *Ostrinia scapulalis* and *Ostrinia furnacalis*, naturally occurring *Wolbachia* kill genetic males. However, genetic males can be rescued and develop as intersexes when their mothers are treated with antibiotics or high temperatures (Kageyama and Traut, 2004; Sakamoto et al., 2008). These observations imply that *Wolbachia* have a feminizing effect that is lethal for *Ostrinia* males. It is unknown how *Wolbachia* interfere with the sex-determining system of insects. However, epigenetic modification is suggested to play an important role in the leafhopper *Zyginidia pullula*, in which naturally-occurring *Wolbachia* cause partial feminization of genetically male individuals. In *Z. pullula*, DNA methylation of the feminized males exhibits a similar pattern with normal females (Negri et al., 2006, 2009).

Not only microorganisms but also nematodes, trematodes and turbellarians can have significant effects on gonad development and/or secondary sexual characters of various arthropods (reviewed by Baudoin, 1975 and references therein). It has been clearly shown that the infection by the mermithid nematode *Gasteromermis* sp. is known to feminize genetic males of the mayfly host *Baetis bicaudatus* morphologically and behaviorally (Vance, 1996).

As described above, various factors are responsible for the generation of intersexes but the individual factors are likely to affect particular steps of a single process of sex determination (Figure 1). Future studies will allow us to reconcile the seemingly various types of intersexes in the context of sex determination and differentiation.

Conclusions

Ever since ancient times, people have been eager to know about the differences between males and females. In some societies, animals with both male and female organs were sanctified and admired. At the present time, such phenomena occurring in insects attract both insect collectors and researchers. The high degree of attention can be inferred from the number of published papers describing gynandromorphism and intersexuality in arthropod species.

However, most of these papers only describe the external morphology of the anomalous individuals. From the scientific perspective, it would be most useful to elucidate the mechanisms that generate gynandromorphs and intersexes in non-*Drosophila* systems, in which the mechanisms of sex determination and differentiation are poorly understood. Indeed, as mentioned above, the great progress made toward elucidating the detailed molecular mechanism of sex determination in *D. melanogaster* is primarily based on the presence of numerous mutant stocks that exhibit intersexual phenotypes (Schutt and Nöthiger, 2000). Since such mutant strains are absent or very rare in other insects, current studies on sex determination basically rely on the cloning of homologous sequences to the sex-determining genes of *D. melanogaster* (e.g., Sievert et al., 1997, Oliveira et al., 2009; Suzuki et al., 2003; but see Beye et al., 2003). In particular, sex reversals (i.e., intersexes) induced by symbiotic microorganisms are often repeatable and controllable under laboratory conditions (Rigaud, 1997; Kageyama and Traut, 2004; Narita et al., 2007a). Elucidation of the molecular mechanisms of such phenomena may allow us to reveal the common mechanism of sex determination among arthropods.

Table 1. Occurrence of individuals having male and female morphologies in arthropods

SUBPHYLUM (CLASS) **ORDER** **Family**	**Species**	**Reference**
HEXAPODA (INSECTA)		
EPHEMEROPTERA		
Baetidae	*Baetis bicaudatus*	Vance, 1996
Polymitarcyidae	*Ephoron leukon*	McCafferty & Bloodgood, 1986
ODONATA		
Libellulidae	*Calopteryx virgo*	Ris, 1929
	Leucorrhinia intermedia	Asahina, 1979
	Nannophya pygmaea	Inoue & Yoshida, 2008
	Sympetrum eroticum	Kagaya & Ukai, 1994
	Sympetrum maculatum	Wada, 2007
	Sympetrum striolatum	Torralba-Burrial & Ocharan, 2009
PLECOPTERA		
Capniidae	*Capnia sequoia*	Nelson & Baumann, 1987
Leuctridae	*Leuctra digitata*	Klotzek, 1971
	Leuctra fusca	Klotzek, 1971; Aubert, 1958
	Leuctra prima	Aubert, 1958
	Paraleuctra	Ricker, 1965
Nemouridae	*Nemoura besametsa*	Nebeker & Gaufin, 1966
	Nemoura cinctipes	Nebeker & Gaufin, 1966
	Prostoia besametsa	Stark et al., 1986
	Protonemura	Sanchez-Ortega, 1992
	Zapada cinctipes	Stark et al., 1986
Notonemouridae	*Austronemoura chilena*	Illies, 1961
ORTHOPTERA		
Acrididae	*Anacridium moestrum*	Potter, 1940
	Camnula pellucida	Paul, 1941; Friauf, 1947

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
	Chorthippus biguttulus	Ebner, 1951; Oschmann, 1971
	Chorthippus longicornis	Karaman, 1959; Oschmann, 1971
	Chorthippus montanus	Bednarz, 1970
	Chorthippus rammei	Ebner, 1940
	Chrysochraon dispar	Brisout de Barneville, 1847, 1848
	Euchorthippus pulvinatus	Descamp, 1968
	Locusta migratoria	Joly, 1959; Verdier, 1960
	Melanoplus adelogyrus	Hubbell, 1932
	Melanoplus differentialis	Slifer, 1966; Slifer & King, 1967
	Melanoplus fasciatus	White & Rock, 1945
	Melanoplus mexicanus	Severin, 1943, 1955
	Oedaleonotus phryneicus	Hebard, 1919
	Oedaleus inormatus	Ritchie, 1978
	Oxya velox	Kimura, 1951
	Pardalophora phoenicoptera	Friauf, 1947
	Podisma pedestris	Baccetti, 1954; Dirsh, 1957
	Podisma sapporoensis	Natori, 1931
	Schistocerca gregaria	Dirsh, 1957; Pener, 1964; Maeno & Tanaka, 2007
	Schistocerca paranensis	Morales Agacino, 1957
	Sphingonotus oaerulans	Dirsh, 1957
	Trimerotropis oitrina x *T. maritima*	Carothers, 1939
	Valanga irregularis	White, 1968
Ephippigeridae	*Ephippiger ephippiger*	Dumortier, 1962
Gryllidae	(*Gryllus argentinus* x *capitatus*) x *G. capitatus*	Cousin, 1967
	(*Gryllus bimaculatus* x *campestris*) x *G. bimaculatus*	Cousin, 1935, 1937
	Gryllus bimaculatus	Johnstone, 1975
	Gryllus bimaculatus x *capitatus*	Cousin, 1963
	Gryllus lineaticeps	Chopard, 1955
	Homoeogryllus japonicus	Ohmachi, 1929, 1932; Suzuki, 1933, 1934
Phaneropteridae	*Isophya pyrenaea*	Dumontier & Paly, 1971
Rhaphidophoridae	*Dolichopoda linderi*	Boudou-Saltet, 1968
Tetrigidae	*Paratettix texanus*	Robertson, 1936
Tettigoniidae	*Amblycorypha oblongifolia*	Pearson, 1927, 1929
	Amblycorypha rotundifolia	Pearson, 1927, 1929
	Aoridopeza reticulata	Agar, 1940
	Barbistes conetrictus	Chladek, 1968
	Barbistes yersini	Brunner von Wattenwyl, 1876
	Decticus albifrons	Boudou-Saltet, 1975

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
	Decticus verrucivorus	Ramme, 1951
	Ephippiger ephippiger	Dumortier, 1962
	Ephippiger terrestris	Kheil, 1914
	Ephippiger vitium	Pantel & de Sinety, 1908
	Insara elegans	Rehn & Hebard, 1914
	Isophya modesta	Kiss, 1960
	Isophya pavelii	Brunner von Wattenwyl, 1876
	Isophya pyrenaea	Dumortier & Paly, 1971
	Leptophyes punctatissima	Cappe de Baillon, 1924, 1932; Carothers, 1939; Chopard, 1955
	Leptophyes punotatissima	Cappe de Baillon, 1924, 1932
	Metrioptera brachyptera	Cappe de Baillon, 1924; Ebner, 1940; Harz, 1960
	Metrioptera brachyptera	Cappe de Baillon, 1924
	Microcentrum retinerve	Nickle, 1983
	Odontura sp.	Chadima, 1872
	Poecilimon elegans	Ramme, 1926
	Poecilimon orbeliscus	Harz, 1967
	Pycnogaster graellsi	Pantel & de Sinety, 1908
	Pycnogaster inermis	Barranco et al., 1995
	Tettigonia viridissima	Klapalek, 1897
	Thmanotrizon fallax	Ramme, 1913
PHASMATODEA		
Bacillidae	*Clonopsis gallica*	Chopard, 1918
Diapheromeridae	*Carausius morosus*	Bergerard, 1958; Pijnacker & Ferwerda, 1980
Phasmatidae	*Extatosoma tiaratum*	Rumbucher, 1974; Calberg, 1981
Phyllidae	*Heteropteryx dilatata*	Brock, 1989; Seow-Choen, 1995
	Phyllium bioculatum	Ziegler, 1989, 1995
	Phyllium celebicum	Grosser, 2003
BLATTODEA		
Blaberidae	*Byrsotria fumigata*	Barth & Bell, 1971
	Gromphadorhina portentosa	Graves et al., 1986
Blattellidae	*Blattella germanica*	Ross & Cochran, 1967
HEMIPTERA		
Cicadellidae	*Zyginidia pullula*	Negri et al., 2006
Cicadidae	*Melampsalta muta*	Dugdale & Fleming, 1966
COLEOPTERA		
Carabidae	*Akimerus schaefferi*	Auvray & Auvray, 1998

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
	Carabus nemoralis	Hartkorn, 1982
	Pterostichus musahiensis	Kashara & Karube, 1995
Cerambycidae	*Ergates faber*	Balazuc, 1952
	Leptura rubra	Weber, 1913
	Rhagium mordax	Starzyk, 1984
Curculionidae	*Euplatypus hintzi*	Beaver, 2000
Dynastidae	*Megasoma elephas*	Dechambre, 1987; Blackaller-Bages & Delgado-Castillo, 1990
Galerucidae	*Cerotoma facialis*	Ruppel, 1971
Lucanidae	*Lucanus elaphus*	Wickham, 1903
Melolonthidae	*Polyphylla fullo*	Vasko, 2008
Salpingidae	*Boros discicollis*	Spilman, 1953
Scarabaeidae	*Cotinis mutabilis*	Deuve, 1992
	Dasylepida ishigakiensis	Tanaka et al., 2006
	Dicranocephalus wallichii	Mizunuma, 2002
	Goliathus cacicus	Ture, 2001
	Golofa tersander	Ratcliffe, 1989
	Polyphylla adspersa	Vasko, 2008
	Polyphylla fullo	Vasko, 2008
	Polyphylla olivieri	Vasko, 2008
	Polyphylla tridentata	Vasko, 2008
Tenebrionidae	*Tribolium castaneum*	Sokoloff & Hoy, 1968
HYMENOPTERA		
Agaonidae	*Blastophaga psenes*	Pereira et al., 2003
	Pegoscapus tonduzi	Pereira et al., 2003
	Tetrapus sp.	R.A.S. Pereira, unpublished data
Andrenidae	*Andrena chengtehensis*	Xu & Cui, 2007
Apidae	*Apis mellifera*	Rothenbuhler et al., 1952; Witherell, 1971; Milne & Rothenbuhler, 1983b; Brockmann & Brückner, 1999
	Nomada sp.	Tsuneki, 1975
	Xylocopa brasilianorum	Gordh & Gulmahamad, 1975
	Xylocopa nigrocincta	Lucia et al., 2009
Chalcididae	*Hockeria rubra*	Halstead, 1992
Diprionidae	*Diprion similis*	Mertins & Coppel, 1971
	Neodiprion sertifer	Heliövaara et al., 1992
Encyrtidae	*Microterys ishiii*	Zhang & Zhu, 2007
Formicidae	*Cardiocondyla emeryi*	Heinze & Trenkle, 1997
	Cardiocondyla kagutsuchi	Yoshizawa et al., 2009

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Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
	Monomorium pharaonis	Berndt & Kremer, 1982
	Pheidole dentata	Jones & Phillips, 1985
	Vollenhovia emeryi	Kinomura & Yamauchi, 1994
Halictidae	*Evylaeus albipes*	Nilsson, 1987
	Megalopta genalis	Wcislo et al., 2004
Megachilidae	*Dianthidium sayi*	Hicks, 1926
	Osmia pentstemonis	Sandhouse, 1923
Pteromalidae	*Nasonia vitripennis*	Kamping et al., 2007
Sphecidae	*Psenulus concolor*	Schneider & Feitz, 2003
	Psenulus laevigatus	Schneider & Feitz, 2003
Tenthredinidae	*Pachynematus clitellatus*	Baker, 1996
	Pteronidea ribesii	Peacock, 1925
Trichogrammatidae	*Trichogramma cordubensis*	Pintureau et al., 1999
	Trichogramma pretiosum	Beserra et al., 2003
DIPTERA		
Anthomyiidae	*Pseudonupedia intersecta*	Blackith & Blackith, 1991
Asilidae	*Nannocyrtopogon minutus*	Cooper, 1990
Ceratopogonidae	*Culicoides crepuscularis*	Smith & Perry, 1967
	Culicoides haematopotus	Smith & Perry, 1967
	Culicoides lailae	Naval, 1969
	Culicoides stellifer	Smith & Perry, 1967
Chironomidae	*Chironomus decorus*	Hubschman & Stack, 1992
	Chironomus tentans	Martin, 1995
Culicidae	*Aedes aegypti*	Antunes & Forattini, 1960
	Aedes albopictus	Barreto et al., 2008
	Aedes canadensis	Roth, 1948
	Aedes cantans	Campbell & Service, 1987
	Aedes craggi	Huang, 1974
	Aedes detrius	Roth, 1948
	Aedes dorsalis	Blakeslee et al., 1966
	Aedes fitchii	Kardatzke, 1978
	Aedes hendersoni	Grimstad & DeFoliart, 1974
	Aedes implacabilis	Roth, 1948
	Aedes mcintoshi	Gargan et al. 1989
	Aedes punctor	Roth, 1948
	Aedes taeniorhynchus	Lum, 1960; Pratt & Sudia, 1964
	Aedes togoi	Chellappan, 1965; Takai & Tadano, 1995
	Aedes triseriatus	Ezenwa & Venard, 1973
	Aedes vexans	Minson, 1969; Oemick, 1976
	Anopheles gambiae	Mason, 1980
	Armigerus subalbatus	Reena & Ramakrishna, 1996
	Culex erythrothorax	Blakeslee & Rigby, 1965
	Culex fuscocephalus	Aslamkhan, 1970

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
	Culex molestus	Roth, 1948
	Culex nigripalpus	Roth, 1948; Meadows, 1966; Barreto et al., 2008
	Culex pedroi	Barreto et al., 2008
	Culex pipiens	Roth, 1948; Blazquez & Maier, 1951; Ausat & Koshi, 1955; Meadows, 1966; Seal, 1966; Ahmad et al., 1985; Ali & Rasheed, 2008
	Culex pseudovishnui	Aslamkhan & Reisen, 1979
	Culex salinarius	Roth, 1948; Meadows, 1966; Hall, 1990
	Culex tarsalis	Rigby, 1966; Rosay, 1968; Mitchell & Hughes, 1969; Harmston, 1971
	Culex tritaeniorhynchus	Aslamkha & Baker, 1969
	Culiseta inornata	Benge, 1970
	Culiseta melanura	Zimmerman & Morris, 1978
	Culiseta morsitans	Howard et al., 2007
	Culiseta novaezealandiae	Dobrotworsky, 1972
	Mansonia dyari	Slaff & Nemjo, 1984
	Orthopodomyia signifera	Roth, 1948
	Taeniorhynchus uniformis	Laurence, 1959
	Theobaldia annulata	Classey, 1942
	Theobaldia annulata	Roth, 1948
	Trichoprosopon digitatum	Lee, 1967
Drosophilidae	*Drosophila melanogaster*	Mavor, 1924; Dobzhansky, 1930; Gowen, 1942; Bonnier et al., 1949; Goldschmidt, 1949; Bonnier & Lüning, 1951; Cook, 1978
	Drosophila pseudoobscura	Dobzhansky & Spassky, 1941
	Drosophila subobscura	Hollingsworth,1955; 1960
	Drosophila virilis	Lebedeff, 1939
Limoniidae	*Dicranomyia mitis*	Geiger, 1983
Muscidae	*Hydrotaea zao*	Iwasa & Shinonaga, 1982
	Musca autumnalis	Cilek & Knapp, 1994
	Musca domestica	Rubini et al., 1980
	Polietina orbitalis	Nihei & Carvalho, 2002
Mycetophilidae	*Sciara ocellaris*	Mori & Perondini, 1980, 1984
Psychodidae	*Lutzomyia davisi*	de Souza et al., 2008
	Lutzomyia rorotaensis	Geoffrey, 1984
	Phlebotomus perniciosus	Gállego et al., 1994

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
	Sergentomyia minuta	Gallego et al., 1991
	Sergentomyia minuta parroti	Harrat et al., 1993; Addadi & Dedet, 1977
Sarcophagidae	*Parasarcophaga harpax*	Kurahashi, 1977
Simuliidae	*Austrosimulium dumbletoni*	Craig & Crosby, 2008.
	Austrosimulium australense	Crosby 1973
	Simulium aokii	Hadi & Takaoka, 1993; Hadi et al., 1994
	Simulium arakawae	Hadi & Takaoka, 1993
	Simulium asakoae	Fukuda et al., 2004
	Simulium auricoma	Grenier & Bertrand, 1950.
	Simulium bidentatum	Hadi & Takaoka, 1993; Hadi et al., 1994
	Simulium damnosum	Cheke & Garms, 1985
	Simulium soubrense	Dang & Peterson, 1979
SIPHONAPTERA		
Ceratophyllidae	*Nosopsyllus henleyi*	Beaucournu & Launay, 1987
LEPIDOPTERA		
Adelidae	*Nemophora rubrofascia*	Hirowatari, 2005
	Lemyra imparilis	Yamauchi, 2000
	Spilosoma mendica	Bocklet, 1909
Bombycidae	*Bombyx mori*	Goldschmidt & Katsuki, 1927, 1931
Crambidae	*Hedylepta accepta*	Riotte, 1979
	Ostrinia furnacalis	Sakamoto et al., 2007
	Ostrinia scapulalis	Kageyama et al., 2003
Geometridae	*Bupalus piniarius*	Kusnezov, 1926
	Paleacrita vernata	Muller, 1968
	Phaeoura mexicanaria	Blanchard, 1969
	Thyrinteina arnobia	Bernardino et al., 2007
Lasiocampidae	*Malacosoma neutria*	Kusnezov, 1926
Lycaenidae	*Lycaeides argyrognomon*	Sashida, 1977
	Lycaena argus	Kusnezov, 1926
	Neozephyrus taxila	Tochikura, 1971
	Strymon bazochii	Riotte, 1979
Lymantriidae	*Lymantria dispar*	Goldschmidt, 1934
Noctuidae	*Agrotis ipsilon*	Gemeno et al, 1998
	Agrotis segetum	Blair, 1976
	Helicoverpa armigera	Josephrajkumar et al., 1998
Nymphalidae	*Argynnis paphia*	Tennent, 2006
	Epinephele tithonus	Bocklet, 1908
	Hyponephele narica	Ivinskis & Saldaitis, 2001
	Ladoga camilla	Beccaloni, 1988

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
Papilionidae	*Ornithoptera croesus*	Parrott & Schmid, 1984
	Ornithoptera priumus	Schmid, 1973
	Ornithoptera victoriae	Schmid, 1973
	Papilio bianor	Waki, 1976
	Papilio glaucus	Scriber & Evans, 1988
	Papilio memnon	Nimura & Otani, 2006
	Papilio polyxenes	Blau, 1978
	Troides rhadamantusrhadamantus	Yamada, 1979
Pieridae	*Colias erate poliographus*	Saitoh, 1955
	Eurema mandarina	Narita et al., 2007a,b
	Gonepteryx cleopatra	Winokur, 2002
	Gonopteryx rhamni	Kusnezov, 1926
	Pieris melete	Takahashi, 1981
	Pieris napi	Kamei, 1970
Pyralidae	*Galleria mellonella*	Smith, 1968
Saturniidae	*Aglia japonica*	Kobayashi, 1997
	Antheraea mylitta	Sen & Jolly, 1967
	Antheraea yamamai	Kawazoe, 1984
	Arsenura armida	Motta, 2000
	Automeris io	Manley, 1971
	Hyalophora cecropia	Bridgehouse, 2000
	Periga circumstans	Moraes, 2005
Satyridae	*Maniola jurtina*	Albrecht, 1993
Sphingidae	*Smerinthus ocellata*	Morgan, 1909
	Smerinthus populi	Morgan, 1909
Tortricidae	*Acleris celiana*	Hodges & Brown, 2007
Yponomeutidae	*Yponomeuta cagnagellus*	Kuijten, 1973
TRICHOPTERA		
Hydroptilidae	*Hydroptila angustata*	Dia & Botosaneanu, 1982
Leptoceridae	*Oecetis ochracea*	Bochert & Bochert, 2005
Limnephilidae	*Anabolia furcata*	Mey, 1982
Psychomyiidae	*Psychomyia ctenophora*	Botosaneanu, 1995
CRUSTACEA (MALACOSTRACA)		
AMPHIPODA		
Gammaridae	*Gammarus chevreuxi*	Sexton, 1924
	Gammarus duebeni	Dunn et al., 1990; Kelly et al., 2004
	Orchestia gammarellus	Ginsburger-Vogel, 1975
DECAPODA		
Coenobitidae	*Coenobita rugosus*	Gusev & Zabotin, 2007
Parastacidae	*Samastacus spinifrons*	Rudolph, 1995, 2002
Potamidae	*Geothelphusa dehaani*	Araki & Matsuura, 1995
	Potamon fluviatile	Micheli, 1991

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
Sergestidae	*Acetes sibogae*	Hanamura & Ohtsuka, 2003
Thalassinidea	*Upogebia stellata*	Pinn et al., 2001
ISOPODA		
Armadillidiidae	*Armadillidiun vulgare*	Juchault et al., 1980, 1991
Asellidae	*Asellus communis*	Smith, 1967
Idoteidae	*Idotea balthica*	Mocquard et al., 1978
MYSIDA		
Mysidae	*Siriella japonica*	Ohtsuka et al., 2003
CRUSTACEA (BRANCHIOPODA)		
ANOSTRACA		
Artemiidae	*Artemia franciscana*	Campos-Rasmos et al., 2006
	Artemia parthenogenetica	Campos-Rasmos et al., 2006
	Artemia salina	Bowen & Hanson, 1962
Chirocephalidae	*Branchinecta lindahli*	Sassaman & Fugate, 1997
CLADOCERA		
Daphniidae	*Daphnia longispina*	Bykova & Markevich, 1979
	Daphnia magna	Mitchell, 2001; Olmstead & LeBlanc, 2007
CHELICERATA (ARACHNIDA)		
ACARI		
Ixodidae	*Ixodes pacificus*	Keirans & Lane, 1997
	Amblyomma cajennense	Labruna et al., 2002
	Amblyomma hebraeum	Clarke & Rechav, 1992
	Amblyomma neumanni	Aguirre et al., 1999
	Amblyomma oblongoguttatum	Labruna et al., 2000
	Amblyomma variegatum	Stampfli, 1985; Balde & Konstantinov, 1994
	Aponomma hydrosauri	Chilton & Sharrad, 1992
	Dermacentor andersoni	Dergousoff & Chilton, 2007; Homsher & Yunker, 1981
	Dermacentor occidentalis	Oliver & Delfin, 1967
	Hyalomma truncatum	Kostrzewski et al., 1986; Clarke & Rechav, 1993
	Rhipicephalus appendiculatus	Mwase et al., 1987
	Rhipicephalus evertsi	Clarke, 1991
	Rhipicephalus sanguineus	Labruna et al., 2002
Phytoseiidae	*Metaseiulus arboreus*	McMurtry & Show, 2007.
ARANEAE		
Linyphiidae	*Centromerus prudens*	Roberts, 1976
Lycosidae	*Schizocosa* sp.	Stratton, 1995
Theridiidae	*Episinus nubilus*	Kumada, 1989

(*Continued*)

Table 1. (*Cont.,*)

SUBPHYLUM (CLASS) ORDER Family	Species	Reference
OPILIONES		
Gagrellidae	*Gagrellula montana*	Tsurusaki, 1982
	Melanopa grandis	Tsurusaki, 1982
Nemastomatidae	*Nemastoma triste*	Thaler, 2004
CHELICERATA (PYCNOGONIDA)		
PANTOPODA		
Ammotheidae	*Cilunculus armatus*	Miyazaki & Makioka, 1993

Note: Not all the published records are shown.

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