

# Juvenile hormone as a physiological regulator mediating phenotypic plasticity in pancrustaceans

Toru Miura 

Misaki Marine Biological Station, School of Science, The University of Tokyo, Miura, Kanagawa, Japan

**Correspondence**

Toru Miura  
Email: miu@mmbs.s.u-tokyo.ac.jp

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Phenotypic plasticity and polyphenism, in which phenotypes can be changed depending on environmental conditions, are common in insects. Several studies focusing on physiological, developmental, and molecular processes underlying the plastic responses have revealed that similar endocrine mechanisms using juvenile hormone (JH) are used to coordinate the flexible developmental processes. This review discusses accumulated knowledge on the caste polyphenism in social insects (especially termites), the wing and the reproductive polyphenisms in aphids, and the nutritional polyphenism and sexual dimorphism in stag beetles. For the comparison with non-insect arthropods, extensive studies on the inducible defense (and reproductive polyphenism) in daphnids (crustacean) are also addressed. In all the cases, JH (and methyl farnesoate in daphnids) plays a central role in mediating environmental stimuli with morphogenetic processes. Since the synthetic pathways for juvenoids, i.e., the mevalonate pathway and downstream pathways to sesquiterpenoids, are conserved across pancrustacean lineages (crustaceans and hexapods including insects), the evolution of developmental regulation by juvenoids that control molting (ecdysis) and metamorphosis is suggested to have occurred in the ancestral arthropods. The discontinuous postembryonic development (i.e., molting) and the regulatory physiological factors (juvenoids) would have enabled plastic developmental systems observed in many arthropod lineages.

**KEYWORDS**

juvenoid, liquid chromatography-mass spectrometry, methyl farnesoate, molting, polyphenism

## 1 | INTRODUCTION: PHENOTYPIC PLASTICITY AND POLYPHENISM

Environments in which organisms reside are not always stable but experience occasional fluctuation in almost all cases. Organisms have adapted to such changeable environments, resulting in the evolution of diverse phenotypic traits over time. Among the interactions between environments and organisms that can affect phenotypic evolution, natural selection and reaction to environments are important. The latter includes phenotypic plasticity (and behavior in animals), which is an ability to flexibly change phenotypes depending

on environmental conditions. Polyphenism is a special case of phenotypic plasticity, in which discrete phenotypes are generated depending on the surrounding environmental conditions (Mayr, 1963; Miura, 2005; Nijhout, 2003; Simpson, Sword, & Lo, 2011; West-Eberhard, 2003). This phenomenon has long been the focus of many studies in development, physiology, ecology, and evolution. In arthropods, especially insects, a number of examples of polyphenism have ever been reported (Gilbert & Epel, 2009), including seasonal, phase, wing, reproductive and caste polyphenism (Nijhout, 2003).

Recent studies have revealed the physiological and molecular underpinnings controlling phenotypic plasticity, mainly in insects.

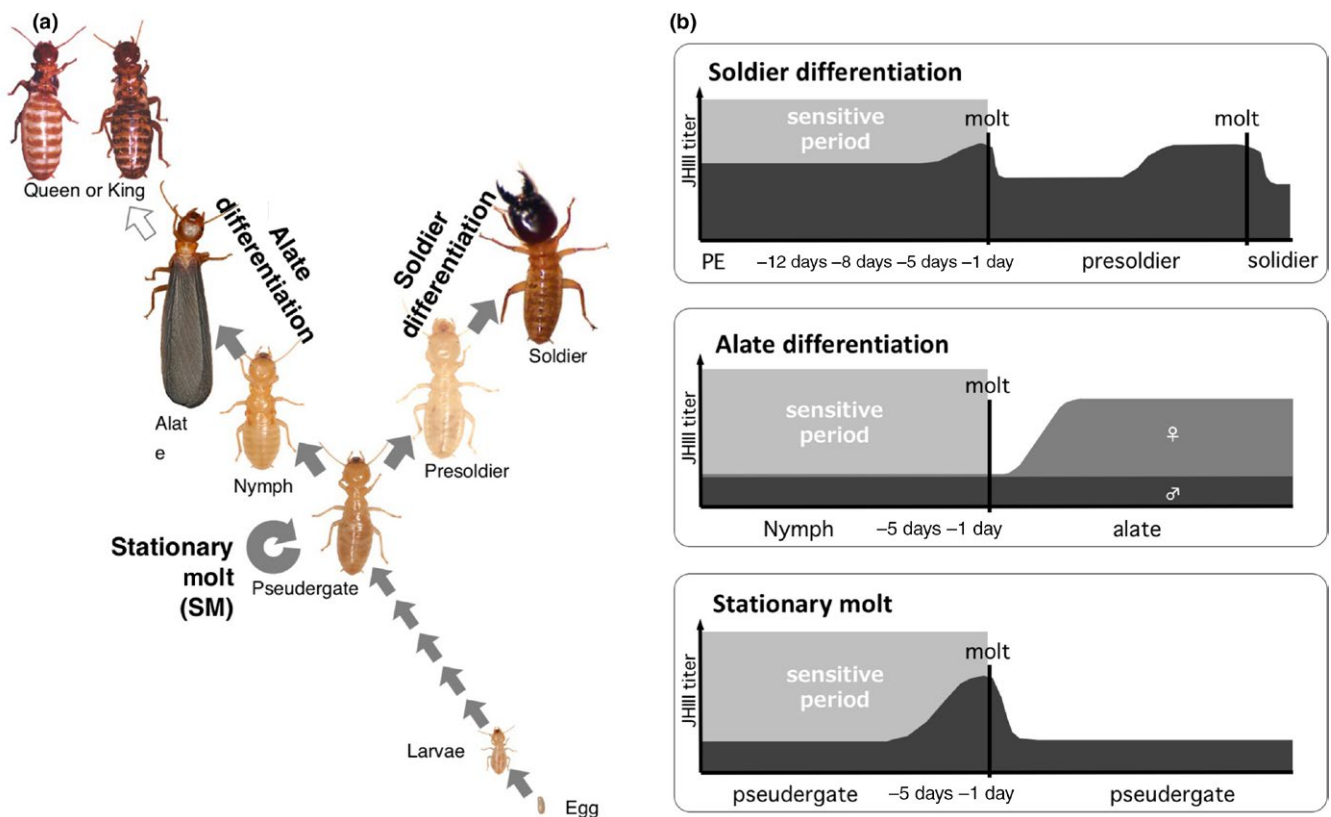
One of the key factors playing major roles in insect phenotypic plasticity is JH, a well-known insect hormone, together with ecdysone (i.e., an important insect hormone that regulates molting and metamorphosis). JH is generally known to have "status-quo" functions in growth and molting during postembryonic development, as the name indicates (Truman & Riddiford, 2002). In addition to the control of developmental timing (i.e., molting), JH also plays multiple roles controlling insect polyphenisms (Hartfelder & Emlen, 2005; Nijhout, 1994). It is known that there are variations of juvenile hormone molecules (Nijhout, 1994). Juvenile hormones 0, I and II (JH 0, JH I, JH II) were discovered in lepidopterans, although juvenile hormone III (JH III) is the most widespread in insects. Later, JHB3 (JH III bisepoxide) was shown to be synthesized in dipterans (Richard et al., 1989). It is also known that methyl farnesoate, a precursor of JH in insects, is used as JH in crustaceans (Homola & Chang, 1997).

In the present review, to identify the shared mechanisms underlying polyphenisms, the current knowledge on the physiological and developmental processes observed in polyphenisms in insects is discussed and compared to those among insect lineages,

including other pancrustaceans such as daphnids. Amongst arthropods, juvenile hormone (JH), a sesquiterpenoid, plays an important role in regulating developmental processes for phenotypic changes. Furthermore, the evolutionary significance of polyphenisms and related physiological mechanisms are discussed.

## 2 | CASTE POLYPHENISM IN SOCIAL INSECTS

One of the most conspicuous examples of insect polyphenism is caste polyphenism, observed in social insects. Two major groups of eusocial insects are social hymenopterans (wasps, bees, and ants) and termites (Lo et al., 2007; Miura, 2005). In social insects, caste fates are determined postnatally, depending on extrinsic factors such as physical environmental conditions (e.g., temperature, humidity, etc.) or social interactions among colony members (Noirot, 1989, 1991). Among various cases of polyphenisms, caste polyphenism is distinctive because of two reasons: (a) the division of labor can be observed among differentiated phenotypes (castes) and (b)



**FIGURE 1** (a) Caste developmental pathways in the damp-wood termite *Hodotermopsis sjostedti*, showing a linear caste pathway (Miura, Hirano, Machida, Kitade, & Matsumoto, 2000; Miura, Koshikawa, Machida, & Matsumoto, 2004). There are seven successive larval instars. The seventh instar plays a role of a worker, although they still possess the potential to develop into alates for their own reproduction. Therefore, individuals in this stage are called "pseudergates" or "false workers." The pseudergates also can differentiate into soldiers and supplementary reproductives (neotenics) and even undergo "stationary molts" to maintain the pseudergate stage. (b) Transitions of juvenile hormone titer during a sensitive intermolt period, which determined caste fates in *H. sjostedti*. Constantly high juvenile hormone (JH) titer induces the soldier differentiation, while low titer induces the alate differentiation. A shift from low to high titer induces the stationary molt. Modified from Cornette et al. (2008)

differentiated phenotypes can act on other colony members as environmental factors, i.e., social interactions.

The physiological and developmental mechanisms underlying caste differentiation in social insects including termites have so far been considered; however, until recently, analyses of the molecular, physiological, and developmental underpinnings have not been performed because of technical difficulties in dealing with non-model animals such as termites. However, recent advances in molecular genetics and genomics have provided tools to analyze such mechanisms in non-model organisms (Miura & Scharf, 2011; Robinson, Grozinger, & Whitfield, 2005).

## 2.1 | Caste differentiation in termites

Termites constitute a major group of eusocial insects belonging to the infraorder Isoptera (or recently revised into the superfamily Termitoidea in the order Blattodea) (Lo et al., 2007). Since termites are hemimetabolous insects, the body plan of juveniles (i.e., nymphs) is similar to those of adults (imagos), except for wings, eyes, and reproductive organs (Miura, 2005). Due to hemimetabolous development, all workers and soldiers are believed to be juveniles, although soldiers are in a terminal postembryonic stage.

The caste differentiation systems, i.e., caste developmental pathways, differ among termite lineages. Based on the differentiation point to reproductive line (into alates) and to neuter line (into workers or soldiers), caste differentiation pathways can be divided into two categories: linear and forked (or bifurcated) pathways (Roisin, 2000). The linear pathways (Figure 1a) are observed in six basal termite families, whereas the forked pathways are observed in three families (Mastotermitidae, Termitidae, and some species of Rhinotermitidae). The evolutionary processes of caste developmental pathways and those of neuter castes have often been argued, although clear agreements have not yet been obtained (Roisin, 2000; Thompson, Kitade, Lo, & Crozier, 2000).

During postembryonic development, the caste developmental fates are determined by extrinsic factors such as physical environment (temperature, humidity, etc.) and/or social interactions among colony members (Noirot, 1991; Watanabe, Gotoh, Miura, & Maekawa, 2014). Social interactions include allo-grooming, trophallaxis, and communications through pheromones and/or antennation. Pheromones affecting the physiological statuses of other individuals are called "primer pheromones," some of which have been identified (e.g., *Reticulitermes speratus*, Matsuura et al., 2010). Although some studies show that genetic factors also affect the caste fate (*Reticulitermes speratus*, Hayashi, Lo, Miyata, & Kitade, 2007; Smith, Toth, Suarez, & Robinson, 2008), it is thought that the tendency of caste differentiation can be changed depending on their genotypes (Schwander, Lo, Beekman, Oldroyd, & Keller, 2010). This means that reaction norms to extrinsic factors can be genetically changeable, as previously proposed (West-Eberhard, 2003). In fact, certain higher termite species (i.e., species belonging to the family Termitidae) produce soldiers from either sex; however, soldiers can be artificially induced from the both sexes (Noirot, 1969).

## 2.2 | Juvenile hormone action in Caste differentiation

In termites, endocrine regulations by JH for hemimetabolous development are also used for the regulation of caste development (Korb, 2015; Korb & Hartfelder, 2008; Miura, 2005). The artificial applications of natural JH and JH analogs are known to induce soldier differentiation (Howard & Haverty, 1979). Based on these previous studies, such as the earliest study performed on *Kaloterme flavicollis* (Lüscher, 1958), a hypothesis was proposed by Nijhout and Wheeler (1982); patterns of JH titer during an intermolt period of larval instars determine the caste fates.

Previously, quantification of intact JH titer has been hindered because of technical difficulties; therefore, the JH titer was inferred based on the size of the *corpora allata*, which secretes JH (Noirot & Bordereau, 1991). Recent improvements in analytical techniques for the quantification of JH titer include radiochemical assay and GC-MS (gas chromatography-mass spectrometry) (Brent, Schal, & Vargo, 2005; Park & Raina, 2004). Additionally, a method using LC-MS (liquid chromatography-mass spectrometry) was developed for more precise quantification of insect JH titer (Westerlund & Hoffmann, 2004).

Recently, there has been an increase in studies monitoring the JH titer during caste differentiation in some termite species (Cornette, Gotoh, Koshikawa, & Miura, 2008; Watanabe, Gotoh, Miura, & Maekawa, 2011). In *Hodotermopsis sjostedti*, a continuously high JH titer during the intermolt period in pseudergates (i.e., false workers that have the potential to differentiate into reproductives) induces soldier differentiation via a presoldier stage, whereas a continuously low titer precedes the alate differentiation through a nymphal stage (Figure 1b; Cornette et al., 2008). A transition from low to high JH titer was observed before the stationary molt. Despite a few inconsistencies, the overall patterns of JH titer transition that precede caste determination have agreed with the hypothesis proposed by Nijhout and Wheeler (1982).

It was also shown in *Zootermopsis nevadensis* that each organ or body part responds to the application of a JH analog differently; the development of alate characteristics such as wings and compound eyes was inhibited by JH application, whereas soldier characteristics, such as mandibles, were extremely exaggerated after JH exposure (Miura, Koshikawa, & Matsumoto, 2003). This indicates that the mechanisms controlling caste-specific organ growth are differentially regulated under the JH pathway, and consequently, the appropriate caste differentiation is accomplished after the reception of various extrinsic factors.

In addition to JH exposure, certain endocrine factors are necessary for caste differentiation in termites. It is known that insulin signaling is upregulated in mandible epithelia, downstream of the JH pathway, before soldier differentiation in *Hodotermopsis sjostedti* (Hattori et al., 2013). Knockdown of the insulin receptor gene suppressed mandibular elongation at the presoldier molt. It is likely that downstream of these endocrine factors, information for the localization of body parts is provided by certain toolkit genes (i.e.,

morphogenetic factors) such as Hox genes. Finally, cell proliferations and/or programmed cell death would occur in a body part specific manner, resulting in caste-specific body patterns (Toga, Yoda, & Maekawa, 2011). Similar caste-specific developmental patterns are also observed in social hymenopterans, such as the wing development of workers and queens in ants (Abouheif & Wray, 2002; Miyazaki et al., 2010; Sameshima, Miura, & Matsumoto, 2004). In addition to morphological differentiation, the nervous system is also modified through caste differentiation (Ishikawa, Aonuma, & Miura, 2008; Ishikawa, Aonuma, Sasaki, & Miura, 2016; Ishikawa et al., 2010), although colony members of the termite society also possess behavioral flexibilities to manage emergencies by behavioral task changes without morphological modifications (Ishikawa & Miura, 2012).

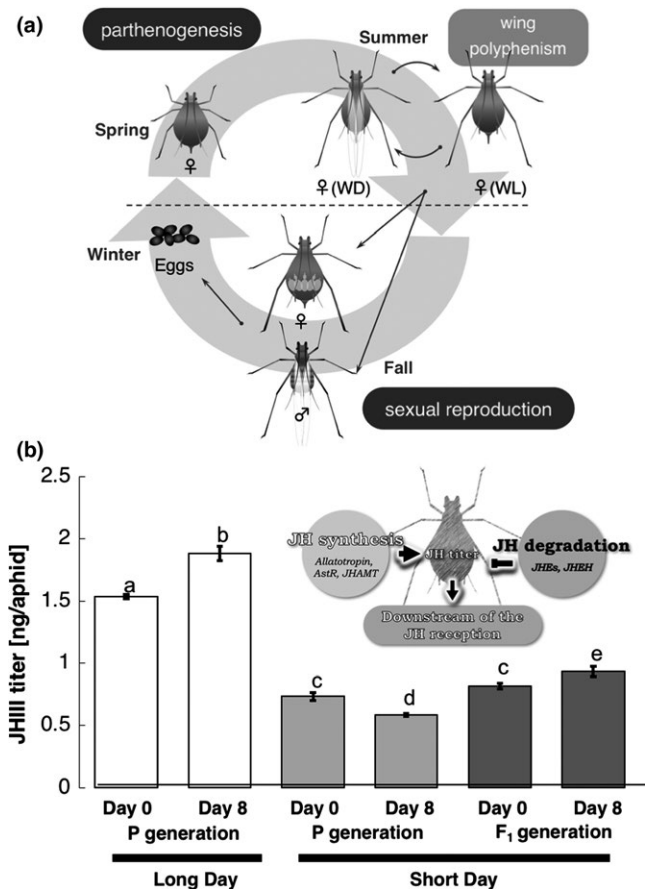
### 2.3 | Polyphenism in other social insects

Among the many cases of polyphenism observed in other insects, it has often been reported that JH is involved in changing phenotypes. In social hymenopterans, JH acts on caste determination during development. In the honeybee, *Apis mellifera*, an increase in larval nutrition, triggers a rise of JH titer in late larval instars, resulting in the development of queens (Hartfelder, Guidugli-Lazzarini, Cervoni, Santos, & Humann, 2015). JH is also known to affect caste determination and/or dominance behavior in stingless and bumble bees (Cnaani, Robinson, & Hefetz, 2000; Hartfelder et al., 2006; Röseler, 1976) and in wasps (Giray, Giovanetti, & West-Eberhard, 2005; Kelstrup, Hartfelder, Nascimento, & Riddiford, 2014; Tibbetts & Izzo, 2009).

Recently, studies on ant species have also accumulated. The sensitive period for JH in queen-worker differentiation varies among ant species; it is later during the larval development in more basal ant species (Penick, Prager, & Liebig, 2012), whereas caste fates are determined early in development (even during embryonic stages) in other species. In *Pheidole*, the queen-worker determination occurs during embryogenesis; however, the differentiation of worker-soldier occurs at the late larval stages (Abouheif & Wray, 2002; Passera & Suzzoni, 1979; Wheeler & Nijhout, 1981). It has been shown in an ant species, *Diacamma* sp., that insulin signaling is also involved in reproductive caste differentiation; it is upregulated in reproductives compared to worker individuals (Okada et al., 2010).

## 3 | APHIDS

Aphids (superfamily Aphidoidea, order Hemiptera) show a variety of polyphenisms including wing polyphenism and reproductive polyphenism (Figure 2a; Dixon, 1998). Some species even produce sterile individuals which function as soldiers (Aoki, 1977). Wing and reproductive polyphenisms are the primary polyphenisms that most aphid species exhibit during their annual life cycles (Dixon, 1998; Miyazaki, 1987). From spring to summer, aphids produce vast numbers of



**FIGURE 2** (a) The annual life cycle of the pea aphid *Acyrthosiphon pisum*. In spring, foundress females that hatch from overwintering eggs start to produce offspring by viviparous parthenogenesis. During summer, progenies can be wingless or winged females which also perform parthenogenesis. Their wing types are determined by environmental conditions such as crowding. In fall, males and oviparous females are produced for sexual reproduction to produce overwintering eggs. (b) Titers of juvenile hormone III (JH III) under long- or short-day length conditions. Under the long-day condition, JH III titer is constantly high. Under the short-day condition, in contrast, the titer becomes lower, that is regulated by JH esterases and JH epoxide hydrolase. In the P generation under short day, males are extensively produced in the late period of larviposition (day 8–). Oviparous females are exclusively produced during the early period (up to day 8) in the F1 generation. Modified from Ishikawa, Ogawa, et al. (2012)

clonal offspring through parthenogenetic viviparous reproduction. Wing polyphenism refers to the production of winged and wingless adult females in response to environmental conditions, such as population density, host-plant quality, and the presence of enemies (Müller, Williams, & Hardie, 2001). During the fall, males and sexual oviparous females produced in response to shorter days mate and produce overwintering eggs (Tagu, Sabater-Munoz, & Simon, 2005) from which parthenogenetic female aphids (foundatrices) hatch during the next spring and subsequently will produce offspring parthenogenetically (Le Trionnaire, Hardie, Jaubert-Possamai, Simon, & Tagu, 2008).

### 3.1 | Aphids: Wing polyphenism

The physiological roles of JH in insect wing development have long been investigated in many taxa such as Orthoptera (Zera & Denno, 1997), Lepidoptera (Miner, Rosenberg, & Nijhout, 2000), and Hemiptera (Iwanaga & Tojo, 1986). Wing polyphenism is one of the major phenomena observed in a diverse lineage of insects. In crickets, JH and its degradative enzyme, JH esterase (JHE), are responsible for the wing polyphenism between brachypterous and macropterous adults (Zera & Denno, 1997). The physiological process under the JH pathway to regulate the wing polyphenisms is suggested to be caused by high JH titer during a sensitive period, which completely or partially inhibits the appropriate development of wings, flight muscles, and other structures for the flight apparatus (Hardie & Lees, 1985a; Nijhout, 1994; Zera & Denno, 1997).

The adaptive reasoning for wing polyphenism in aphids is to change their reproductive and dispersal strategies; winged aphids are produced for the host-plant alteration, induced by many ecological factors, mainly, density and host-plant quality (Müller et al., 2001). The differentiation between winged and wingless aphids occurs at early nymphal stages, probably during the first-instar nymph, supported by the presence of wing primordia at their meso- and meta-thoraces during the first instar, even in wingless aphids (Ishikawa, Hongo, & Miura, 2008). In the pea aphid, *Acyrtosiphon pisum*, a toolkit gene *apterous1*, was shown to be differentially expressed at early instars. *Apterous1* is highly expressed in future winged aphids (Brisson, Ishikawa, & Miura, 2010). In winged adults, flight muscle breakdown after their dispersal flight is also under the regulation of JH (Kobayashi & Ishikawa, 1994).

In a strain of the vetch aphid *Megoura crassicauda*, winged aphids can easily be induced by a high density conditions; therefore, some molecular studies have been conducted using this species. In this species, the high density condition induces differential expressions of several genes including the *wingless* gene, thereby producing winged offspring (Ishikawa, Ishikawa, et al., 2012). In addition, the JH III titer at the third-instar nymphs was higher in the presumptive wingless aphids than the winged aphids (Ishikawa, Gotoh, Abe, & Miura, 2013). Furthermore, the application of JH III on third-instar nymphs disturbed their appropriate wing development, leading to winged/wingless intermorphs or juvenilized aphids with supernumerary molts (Ishikawa et al., 2013).

In some strains of *A. pisum*, genetic wing polymorphism is observed among males. A single locus on the X chromosome called “*aphicarus*” (*api*) is known to be responsible for the genetic polymorphism and can also be involved in female wing polyphenism (Braendle, Friebe, Caillaud, & Stern, 2005).

### 3.2 | Aphids: Reproductive polyphenism

During reproductive polyphenism, aphids alter their reproductive modes from parthenogenetic viviparous reproduction to sexual oviparous reproduction, due to short day lengths and low temperature conditions (Dixon, 1998). To trigger the switch from parthenogenesis

to sexual reproduction, long night length is believed to be required, and low temperature modifies the effect (Hardie, 1981; Lees, 1973). It was demonstrated that the photoperiod is sensed by five neurosecretory cells in the protocerebrum of aphid brain, through head-capsule cuticle (Lees, 1964, 1981; Steel & Lees, 1977).

It is also known that JH III plays important roles in reproductive polyphenism (Hardie & Lees, 1985b; Ishikawa, Ogawa, et al., 2012; Ishikawa et al., 2013). For example, the volume of corpora allata was different between long- and short-day reared vetch aphids *Megoura viciae* (Hardie, 1987). Even under short-day conditions, when JH and its analogs were topically applied on aphids, parthenogenetic reproduction was induced (Corbitt & Hardie, 1985; Hardie & Lees, 1985a,b; Lees, 1981). Consistently, the treatment of precocene, a chemical that is known to damage corpora allata and inhibit the JH synthesis, induced male production in *Myzus persicae* (Hales & Mittler, 1983, 1988). Quantification of JH titer was recently conducted by GC-MS, although the sensitivity was technically low (Hardie, Baker, Jamieson, Lees, & Schooley, 1985). A recent study in *A. pisum* quantified JH titer in response to short-day length using LC-MS, revealing that the JH titer in aphids reared under short-day conditions was lower than under long-day conditions and that this lowering of JH induced by short-day length was suggested to be caused by the expression of genes responsible for JH degradation (i.e., genes encoding JH esterases and JH epoxide hydrolase; Figure 2b; Ishikawa, Ogawa, et al., 2012).

In both the wing and the reproductive polyphenisms, at least in Macrosiphini aphids such as *A. pisum* and *M. crassicauda*, the trans-generational developmental regulation through viviparity is suggested to be important (Ogawa & Miura, 2014). In addition to these aphid polyphenisms, some aphid species also produce soldier caste (Tian & Zhou, 2014). Although it is not well studied, JH is suggested to be involved also in the production of aphid soldiers.

## 4 | SEXUAL DIMORPHISM AND NUTRITIONAL POLYPHENISM IN BEETLES

In many of the coleopteran species, especially in the superfamily Scarabaeoidea, sexual dimorphism is observed in adults. In almost all cases, adult males possess enlarged weapons or ornamentation to obtain females through competition or mate choice; therefore, these strategies have exaggerated sexually selected traits (Williams & Carroll, 2009). Sex-specific exaggerated traits often develop in a condition-dependent manner; in other words, these traits are also cases of phenotypic plasticity or polyphenism (Emlen, 2008; Emlen & Nijhout, 2000). The size and shape of male weapons in the species show phenotypic plasticity (polyphenism), depending upon nutritional conditions during their larval development. In the case of dung beetles, well-fed male larvae become adults possessing horn(s) on their heads and/or thoraces (Emlen & Nijhout, 1999, 2001; Emlen, Warren, Johns, Dworkin, & Lavine, 2012). Several studies in the dung beetle genus *Onthophagus* showed that JH mediates the nutritional condition during larval development (Emlen & Nijhout, 1999, 2001),



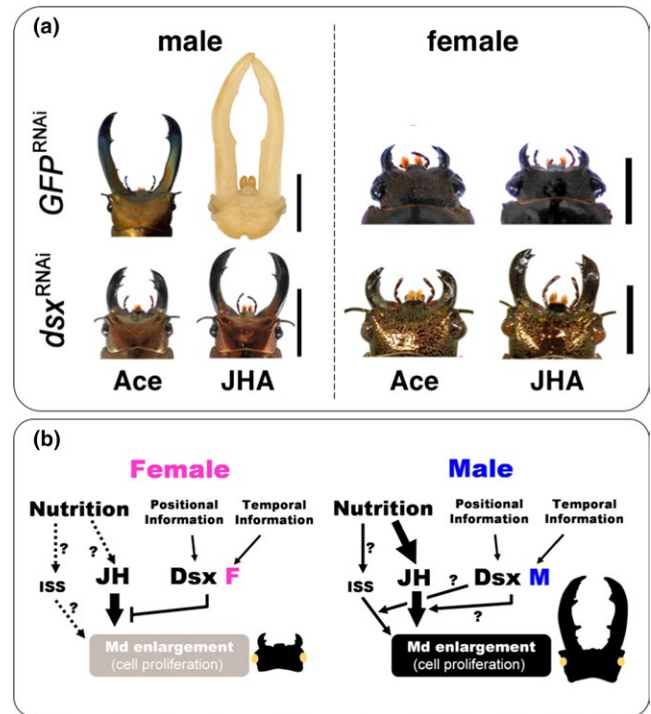
resulting in differential gene expressions of some toolkit genes (Moczek & Nagy, 2005). It has also been shown by the application of JH analog that there are two different sensitive periods: (a) larval growth and (b) horn development (Emlen & Nijhout, 1999, 2001). In addition to the JH pathway, the insulin signaling pathway is suggested to play important roles mediating nutrition and development in *Onthophagus* (Emlen, Szafran, Corley, & Dworkin, 2006).

As in the horned beetles, the JH pathway has been implicated in a stag beetle *Cyclommatus metallifer*, in which males possess extremely enlarged mandibles, with some variation among individuals (Gotoh et al., 2011). This study showed a clear correlation between JH titer and mandibular growth and identified the sensitive period (early stage of prepupa, i.e., a developmental stage just before pupation) of JH stimulation for mandible growth. The topical application of a JH analog (fenoxycarb) during the sensitive period unnaturally enlarged their mandibles (Figure 3). The results are consistent with those shown in *Onthophagus*.

To explain why phenotypic plasticity caused by nutritional conditions was only observed in males, a study revealed the relationship between sex determination and the JH pathway in *C. metallifer* (Gotoh et al., 2014). When the *doublesex* gene, one of the important sex determination factors encoding transcription factors that regulate the development of sex-specific traits, was knocked down, adults of both sexes showed intermediate morphologies between males and females. The application of a JH analog to the knocked-down prepupae of female stag beetles also induced exaggerated mandibular growth at the time of pupation (Figure 3). The study first demonstrated a causal link between sex determination and the JH signaling pathway, leading to sex-specific nutrition-dependent plasticity. In addition, in *C. metallifer*, a successive study showed that the Fat/Hippo signaling pathway coordinates the link between the whole-body hormonal signal (JH) and tissue specific developmental pathways (e.g., patterning genes or toolkit genes; Gotoh et al., 2015).

## 5 | PHENOTYPIC PLASTICITY IN CRUSTACEANS

Phenotypic plasticity and polyphenism are observed in arthropods other than insects. The most prominent example is the inducible defense or defense polyphenism in a crustacean lineage, daphnids (order Cladocera, class Branchiopoda, subphylum Crustacea). Prey organisms show a number of defensive strategies to avoid attacks by predators. In particular, it is difficult for planktonic or sessile animals to rapidly escape from predatory attacks; therefore, these animals often possess defensive morphologies under the presence of predators (Adler & Harvell, 1990; Tollrian & Harvell, 1999). The water flea *Daphnia* produces defensive morphology in response to chemical cues released by predators, so-called "kairomones" (Tollrian & Dodson, 1999). Seasonal changes of *Daphnia* morphology have long been known as "cyclomorphosis," which later turned out to be triggered by seasonal appearances of predators (Dodson, 1989; Woltereck, 1909).



**FIGURE 3** (a) Results of RNAi experiments of the *doublesex* (*dsx*) gene in a stag beetle *Cyclommatus metallifer*, indicating the link between sex determination and the juvenile hormone (JH) pathway. In controls (*dsRNA* of the *GFP* gene was injected), only males respond to the JHA application by exaggerating their mandibles, whereas female mandibles do not show any extra growth. However, when the *dsx* gene was knocked down (*dsx*<sup>RNAi</sup>), even female mandibles responded to the JHA application. (b) Schematic diagram showing the link between the JH pathway and the sex determination cascade. In females, unlike males, *dsx* suppresses the JH action that mediates nutritional conditions. Modified from Gotoh et al. (2014)

### 5.1 | Inducible defense in daphnids

Defense strategies of *Daphnia*, such as defensive morphs, life-history, and behavioral changes, are well studied and their adaptive significance has been discussed (Tollrian & Dodson, 1999). Among *Daphnia* species, *D. pulex*, the most famous and widely distributed species, produces neckteeth at the occipital region of the head in response to kairomones released by their predators, phantom midges (*Chaoborus* larvae). This structure can act as an obstacle preventing predators from swallowing the daphnids, thereby decreasing the predation risk (Dodson, 1974; Laforsch, Ngwa, Grill, & Tollrian, 2004; Miyakawa, Sugimoto, Kohyama, Iguchi, & Miura, 2015; Tollrian & Dodson, 1999).

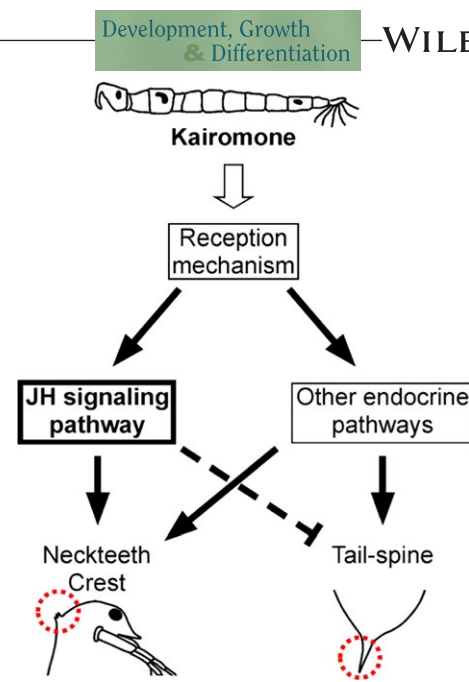
During postembryonic development, the neckteeth begin to form at the first instar, and the number of neckteeth spines reaches a maximum at the third instar (Imai, Naraki, Tochinal, & Miura, 2009). It is also known that the formation of neckteeth requires some costs in development and/or reproduction; there are tradeoffs between the neckteeth formation and the developmental rate or the number of offspring (Imai et al., 2009). The exposure to kairomones during embryonic stages is

known to be required for neckteeth formation at juvenile stages (Imai et al., 2009; Krueger & Dodson, 1981; Parejko, 1992). For neckteeth formation in response to predator kairomones, it is suggested that some neuronal transmissions and endocrine pathways mediate kairomone reception and neckteeth morphogenesis (Barry, 2002; McCool, Baer, & Christie, 2011; Weiss, Kruppert, Laforsch, & Tollrian, 2012). Recent advances of genomic, genetic, ecological, and toxicological studies in daphnids have enabled us to understand molecular and physiological underpinnings of the inducible defense (Eads, Colbourne, Bohuski, & Andrews, 2007; Jenner & Wills, 2007).

Methyl farnesoate (MF) is a precursor of JH III and is thought to be a candidate molecule for innate JH in crustaceans, supported by the fact that the *D. pulex* genome lacks an ortholog for CYP15A1, an epoxidase catalyzing MF to JH III (Miyakawa, Toyota, Symiya, & Iguchi, 2014). Some genes related to JH synthesis and JH reception, i.e., *JH acid methyltransferase (JHAMT)* and *methoprene-tolerant (Met)*, were shown to be upregulated in response to predatory kairomone exposure (Miyakawa et al., 2010). Furthermore, the applications of some juvenoids (MF, JH III, fenoxycarb) were shown to stimulate or enhance defense formation (Miyakawa, Toyota, et al., 2013; Oda, Kato, Watanabe, Tatarazako, & Iguchi, 2011). However, these juvenoids did not accelerate the elongation of the tail spine, which is normally elongated in response to kairomone exposure, suggesting that there are other physiological mechanisms coordinating the phenotype of the defensive morph (Figure 4; Miyakawa, Gotoh, Sugimoto, & Miura, 2013).

## 5.2 | Reproductive polyphenism in daphnids

In addition to the inducible defense, daphnids also show a reproductive polyphenism. Similar to other cladocerans, daphnids also change their reproductive modes from parthenogenetic clonal reproduction to sexual reproduction, so-called “cyclic parthenogenesis” (Hebert, 1987). Under favorable conditions with abundant resources, female daphnids produce clonal offspring by parthenogenesis (Hebert, 1978; Lynch & Gabriel, 1983). In response to unfavorable conditions with diminishing resources, such as starvation or crowding, male adults are produced by parthenogenesis, and mate with females, resulting in the production of fertilized diapausing eggs encased in a protective ephippium (Hebert, 1978; Kleiven, Larsson, & Hobaek, 1992). Multiple studies have shown that male production is induced by applications of juvenoids, suggesting that the JH pathway mediates sex determination in *Daphnia* in response to environmental stimuli (Eads, Andrews, & Colbourne, 2008; Oda, Tatarazako, Watanabe, Morita, & Iguchi, 2005; Olmstead & Leblanc, 2002; Tatarazako, Oda, Watanabe, Morita, & Iguchi, 2003). The physiological coordination of environmental conditions probably regulates a sex-determination gene, *doublesex*, resulting in the sex determination of developing embryos (or oocytes) and leading to the formation of males in *Daphnia* (Kato, Kobayashi, Watanabe, & Iguchi, 2011). In addition to the inducible defense and the reproductive polyphenism, hemoglobin induction by environmental stimuli is also suggested to be mediated by the JH pathway (Eads et al., 2008).



**FIGURE 4** Schematic diagram showing the physiological regulations of the inducible defense in *Daphnia pulex*. Although molecular structures of the hormone are different between insects and daphnids, the juvenile hormone (JH) signaling pathway mediates the predator-induced polyphenism. The JH pathway is suggested to be required for the neckteeth formation, although it is not sufficient to complete morphogenesis for the inducible defense. Modified from Miyakawa, Gotoh, et al. (2013)

## 6 | EVOLUTION OF PHENOTYPIC PLASTICITY AND THE JH SIGNALING

In this review, I summarize recent advances in the study of phenotypic plasticity and polyphenism in insects and daphnids, that are classified into the Pancrustacea. In almost all the cases, these animals utilize juvenoids (JH and MF) as the physiological or endocrine regulator(s) for phenotypic changes in response to environmental changes. This also indicates that developmental regulation of molting or ecdysis should be required for the phenotypic changes. Considering the evolutionary processes of the JH pathways; the conserved mevalonate pathway had already existed in the bilaterian ancestor in the Ordovician period (440–500 mya; Bellés, Martin, & Piulachs, 2005; Cheong, Huang, Bendena, Tobe, & Hui, 2015; Tobe & Bendena, 1999). In addition, MF has been widely identified in Arthropoda, i.e., chelicerates, crustaceans, and insects (Cheong et al., 2015). In chelicerates, innate farnesol (the precursor of MF and JH) has been identified in mites and ticks (Grbić et al., 2011; Regev & Cone, 1975; Roe et al., 1993). Therefore, the synthetic pathways downstream of the mevalonate pathway have been evolutionarily conserved in the pancrustacean lineage (Cheong et al., 2015).

As mentioned above, furthermore, same genes and genetic cascades are involved in the JH action in different lineages, such as insulin signaling pathway (termites, ants and dung beetles), a sex-determination factor *dsx* (stag beetles and daphnids). Some other studies in beetles also showed that these factors were involved

in the development of plastic weapon characters (insulin signaling in rhinoceros and dung beetles, Emlen et al., 2012; Snell-Rood & Moczek, 2012; *dsx* in dung beetles and rhinoceros beetles; Kijimoto, Moczek, & Andrews, 2012). As for caste differentiation in termites, function of genes involved in the JH synthesis (*JHAMT*) and the receptor gene (*Met*) were also reported in different species (Yaguchi, Masuoka, Inoue, & Maekawa, 2015). These commonalities regulating plastic traits might indicate that the shared pre-existing mechanisms controlling the physiological and developmental conditions would be applied to the developmental regulations of phenotypic plasticity.

In crustaceans, MF is suggested to be one of the main sesquiterpenoids controlling development and reproduction by regulating the physiological status (Laufer, Demir, Pan, Stuart, & Ahl, 2005; Nagaraju & Borst, 2008; Tamone & Chang, 1993; Yamamoto et al., 1997). Other than daphnids, the crab *Carcinus maenas* can switch carapace color patterns in response to environmental stresses. MF is involved in this plastic transition of color phenotypes (Lewis, 2011; Nagaraju & Borst, 2008; Reid, Abello, Kaiser, & Warman, 1997). In barnacles, the metamorphosis from cyprid larvae to sessile adults is induced by high MF titer (Smith et al., 2000; Yamamoto et al., 1997). Considered together, the ancestral roles of MF in regulating molting, metamorphosis, and phenotypic plasticity in pancrustaceans are suggested.

Although information on juvenoid functions in myriapods is lacking, several studies suggest its role in phenotypic plasticity in determining segment number in a centipede *Strigamia maritima* (Vedel, Chipman, Akam, & Arthur, 2008). The number of segments of this centipede species depends on rearing temperature, and the sensitive period is found to be the blastoderm stage, at the onset of segmentation during embryogenesis. Interestingly, this species shows a latitudinal cline; centipedes in southern populations possess more segments (Kettle, Johnstone, Jowett, Arthur, & Arthur, 2003). The variation of segment number among populations is also explained by some heritable components, suggesting the link between phenotypic plasticity and genetic variations (Vedel, Brena, & Arthur, 2009). Juvenoids do not only function during postembryonic development, but affect embryogenesis as shown in the case of caste differentiation in ants (Nijhout & Wheeler, 1982). Therefore, in the centipede segmentation, endocrine factors such as MF could modulate the link between environmental conditions (temperature) and the genetic patterns of segmentation.

As for the evolution of phenotypic plasticity and polyphenism, an intriguing study in a tobacco hornworm, *Manduca sexta*, clearly showed that the JH titer mediated the evolution of reaction norm patterns (Suzuki & Nijhout, 2006). In the experiments, the reaction norms of larval color that can be induced by heat-shock treatments were shown to have evolved by selection through generations. They also showed that JH titer responding to the temperature shifts was responsible for the color changes. Therefore, similar physiological mechanisms that mediate temperature shifts might exist in both arthropod lineages (i.e., myriapods and insects).

In arthropods or ecdysozoans, molting (ecdysis) has generally evolved to allow for discontinuous growth. Additionally, the acquisition of molting has enabled drastic morphological changes such

as metamorphosis. In general, the processes of animal growth are affected by environmental conditions such as food availability and temperature; therefore, the regulation of moltings would allow for flexibility in development. Drastic phenotypic changes in response to environments are enabled by the arthropod-specific developmental patterns that are not only spatially modular, i.e., segmented body plans, but also temporally modular, i.e., moltings.

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## ORCID

Toru Miura  <http://orcid.org/0000-0002-7456-4402>

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