

Development and evolution of insect polyphenisms: novel insights through the study of sex determination mechanisms

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Polyphenism is defined as a single individual's ability to develop into two or more alternative phenotypes. Polyphenic development is taxonomically widespread among insects, cued by diverse environmental factors, and enables single genotypes to accommodate breathtaking phenotypic diversity. Most research on the developmental regulation and evolution of insect polyphenisms has focused on endocrine control mechanisms, in particular the role of the sesquiterpenoid juvenile hormone. Here we review recent findings that suggest additional and previously overlooked mechanisms that underlie the developmental regulation and rapid evolution of polyphenic development. Specifically, we focus on the role of somatic sex determination mechanisms, which mediate body-region and tissue-specific differentiation as a function of sex across insects. Recent work on *Onthophagus* horned beetles suggest that the same mechanisms have been co-opted to regulate the development of nutritionally cued, alternative male morphs, and that rapid changes in these mechanisms underlie rapid evolutionary changes in patterns of phenotype expression across *Onthophagus* species, including the loss of old and gain of novel locations for horn development, the evolution of reversed sexual dimorphisms, and the secondary loss of male polyphenism. We discuss how these findings expand the way we think about the origins and diversification of polyphenisms, and close by briefly highlighting potentially fruitful avenues for future research.

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Introduction — a brief primer on insect polyphenisms

Polyphenic development enables a single individual or genotype to give rise to two or more discrete phenotypes depending on environmental conditions [1]. Polyphenic development is found across phyla, and reaches some of

its most extreme manifestations within the insects [2]. Well-known examples include seasonal polyphenisms in the Lepidoptera, phase polyphenisms in locusts, alternations between sexual and asexual reproductive modes in aphids, castes in social insects, wing polyphenisms in crickets or alternative fighter and sneaker morphs in many beetles (reviewed in [1,3]). Polyphenic development can be responsive to a wide range of cues, as well as combinations thereof, from photoperiod and nutrition to social conditions and host plant age [4]. Lastly, polyphenic development entails the coordinated, and typically adaptive, divergence of syndromes of traits: for example, social insect castes not only differ in size and shape, but also in relative investment into reproductive structures, energy metabolism, and behavioral repertoire [5,6]; likewise, seasonal butterfly morphs diverge not just in wing patterns, but also in wing shape, flight and hiding behavior, and mate preferences [1,7,8]. As such, polyphenic development enables individuals to develop into strikingly different, yet highly functionally integrated, phenotypes to suit diverse ecological conditions.

Most research on the developmental regulation and evolution of insect polyphenisms has focused on endocrine control mechanisms, in particular the role of the sesquiterpenoid juvenile hormone (JH) [9–11]. Juvenile hormone plays a fundamental role in the regulation of metamorphosis, where its presence or absence during nymphal and larval instars determines whether developing animals molt into the same developmental stage (e.g. larva-to-larva) or transition to the next stage (e.g. larva-to-pupa, or pupa-to-adult), respectively, a capacity that has earned JH the synonym status quo hormone [9]. Numerous studies have now well established that aspects of JH signaling have been co-opted into the regulation of polyphenic development (reviewed in [4,11]) and that evolutionary changes in JH metabolism and ontogenetic timing of tissue sensitivity to circulating JH underlie evolved changes in polyphenic development in artificially selected or naturally evolved populations and species (e.g. [12–15]). Very recent studies on polyphenic beetles now suggest that somatic sex-determination mechanisms have undergone a partly parallel evolutionary journey: from regulating basic and fundamental aspects of insect development to their secondary co-option into the context of polyphenic differentiation [16*,17*].

Somatic sex-determination in insects — the role of doublesex

In insects, the sex determination pathway regulates the sex-biased expression of downstream target genes, which

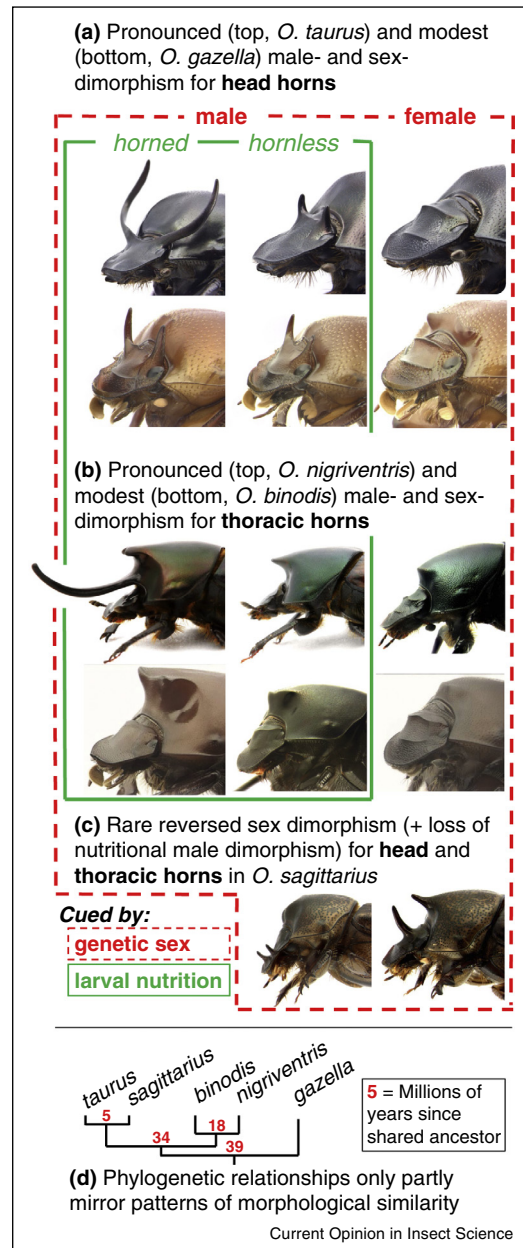
in turn facilitates the expression of sex-specific development and behavior across diverse insects [18–20]. The transcription factor Doublesex (Dsx) plays a particularly significant role in this pathway, which is best understood from studies in *Drosophila*. In *D. melanogaster*, a hierarchy of sex-determination genes acts to regulate the expression of male- and female-specific splice variants of *dsx*, which in turn regulate the sex-biased expression of downstream target genes responsible for the elaboration of sexually dimorphic traits [21]. Even though the sex-determination pathway *upstream* of *dsx* is surprisingly divergent across insect orders, *dsx* itself is highly conserved, including most notably the expression of male- and female-specific transcription factors generated via alternative splicing [19,20].

Furthermore, recent work has shown that *dsx* is a nexus for the evolution and diversification of sexually dimorphic traits, either via changes in *cis*-regulatory sequences of *dsx* target genes [22,23] or changes in the expression of *dsx* itself [24,25]. Additionally, the recognition that developing *Drosophila*, and likely most insects in general, are mosaic for *dsx* expression, and thus are mosaic for the potential to differentiate sexually, has led to a greater appreciation for the potential of evolutionary diversification of sexual dimorphisms through tissue- and body region-specific changes in *dsx* activity [26]. Recent studies on horn-polyphenic beetles now suggest that *dsx*-mediated regulation of development has been recruited into the regulation of *nutrition*-specific differentiation of alternative horned and hornless fighter and sneaker morphs.

Sex- and morph-specific development in horn-polyphenic beetles may be regulated via differential expression of sex-specific Doublesex isoforms

Horn and horn-like structures have evolved in at least seven beetle families, where they function as weapons of sexual selection (reviewed in [27]). Horn development is highly variable within and between sexes as well as among species, and is heavily influenced by both genetic (e.g. sex) and environmental factors (e.g. nutrition; Figure 1). For instance, in nearly all species horn development is restricted to males and absent in females [28]. Female hornlessness arises as a consequence of canalized sex-specific development, most likely following XX/XY sex determination (males are XY, e.g. [29]) and is not affected by nutritional conditions: in these cases all females, regardless of larval nutrition and resulting adult body size, are hornless. In contrast, horn development in males is not nearly as canalized, and is frequently influenced by nutritional conditions (e.g. [30–32]). In many species, variation in larval nutrition cues the expression of distinct, alternative horned (large) and hornless (small) morphs among males. In these cases, male phenotype is the result of developmental plasticity: all males have the capacity to develop into either morph, but choose one or

Figure 1



Phenotypic diversity among five *Onthophagus* species and their phylogenetic relationships. **(a)–(c)** Diversity in sexual-dimorphisms (red box, cued by genetic sex) and male-dimorphisms (green box, cued by nutrition). **(d)** Phylogenetic relationships among the same five species, which only partly mirror patterns of morphological similarity [35].

the other pathway depending on feeding conditions encountered during larval development. Importantly, the resulting alternative morphs differ not only in the presence of elaborate horns, but in a whole syndrome of co-diverging morphological, physiological, and behavioral phenotypes, ranging from reproductive tactics, aggression and paternal investment to testes development and thermoregulatory behavior [16*,27]. Lastly, species have

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