Insect oogenesis and its physiological control

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Abstract

Insect females produce many eggs over their lifetime, contributing to the evolutionary success of this large and diverse group of animals. In this chapter, we provide an overview of oogenesis and its environmental and physiological regulation in multiple insect species—including the major model insect *Drosophila melanogaster*—to illustrate the wealth of biological knowledge that can be gained from their study. We describe different types of ovary morphology and major adult oogenesis processes from the earliest stages to the formation of mature oocytes. We also cover the influence of diet, temperature, mating, microorganisms, social interactions, and sensory inputs, as well as some of the key physiological signals, such as juvenile hormone, ecdysteroids, and insulin signaling, that orchestrate the ovarian response to various inputs. We conclude by highlighting open questions and the importance of continued research on the fascinating biology of insect oogenesis, a topic with key ecological, agricultural, and medical implications.

Keywords: Diet; ecdysone; germline cyst; germline stem cell; egg chamber; follicle; insulin; juvenile hormone; mating; microorganisms; nurse cell; oocyte; temperature; trophocyte; vitellogenesis

Key points

- Description of three types of ovarioles: panoistic, polytrophic meroistic, and telotrophic meroistic
- Description of germline stem cells or precursors, follicle formation, and oocyte growth and development, including vitellogenesis and eggshell formation
- Overview of effects of diet, temperature, microorganisms, social interactions, and sensory inputs on oogenesis
- Overview of major physiological pathways, including juvenile hormone, ecdysteroids, insulin signaling, target of rapamycin, Venus kinase receptor, AMP-dependent kinase, and additional interorgan communication regulating egg production

Introduction

The evolutionary success of insects is driven by their remarkable reproductive prowess (Klowden, 2013). Over a million species are known in the class Insecta, with holometabolous insects making up ~50% of all animal and plant species and ~83% of insects (Schmidt-Ott and Lynch, 2016). Most insect females can produce hundreds to thousands of eggs, such that oogenesis (i.e., egg production) represents a substantial investment of resources and energy by these females. It is also interesting to note that although most insects are oviparous (i.e., females lay eggs), there are multiple instances of either facultative or obligate viviparity (i.e., females give birth to live offspring) among at least 13 orders of insects (Benoit *et al.*, 2015, 2025). Tsetse flies *Glossina* spp. (Diptera) represent a rare example of adenotrophic viviparity, meaning that embryos and larvae develop in the uterus and are nourished through specialized secretions (Benoit *et al.*, 2015). The tight regulation of oogenesis according to environmental inputs and physiological changes is crucial for the success of insect species. In this chapter, we provide an overview of insect ovarian anatomy and major processes required for oogenesis and describe key aspects of the environmental and physiological control of these processes. We also highlight open questions and the importance of investigating insect oogenesis. We cover insects in various orders, including Diptera, Lepidoptera, Hymenoptera, Coleoptera, Hemiptera, Orthoptera, and Blattodea (Table 1)—with a focus on the best studied species, the fruit fly *Drosophila melanogaster* (Diptera).

Table 1 **List of insect species included in this chapter**

Ovariole	Order	Species	Common name	Relevance beyond basic science, biodiversity, and ecology
Panoistic	Blattodea	*Blattella germanica*	German cockroach	Allergenic (Yu et al., 2024); salmonella carrier (Pinarelli Fazion et al., 2023)
		Periplaneta americana	American cockroach	Allergenic (Yu et al., 2024); medicinal (Zhou et al., 2022)
		Reticulitermes speratus	Japanese termite	–
	Orthoptera	*Acheta domesticus*	House cricket	Edible (Nachtigall et al., 2025)
		Gryllus lineaticeps	Field cricket	–
		Locusta migratoria	Migratory locust	Edible (Nachtigall et al., 2025); agricultural pest (Peng et al., 2020; Klein et al., 2021)
		Schistocerca gregaria	Desert locust	Agricultural pest (Peng et al., 2020; Klein et al., 2021)
		Isophya nervosa	Bush cricket	–
		Stenocatantops splendens	Grasshopper	–
	Mantodea	*Ciulfina klassi*	Praying mantis	–
	Mecoptera	*Nannochorista neotropica*	Scorpion fly[a]	–
	Zygentoma	*Thermobia domestica*	Firebrat	–
Polytrophic meroistic	Diptera	*Aedes aegypti*	Egyptian mosquito, dengue mosquito, yellow fever mosquito	Vector of dengue virus, yellow fever, virus, chikungunya virus, Zika virus, West Nile virus, St. Louis encephalitis virus (Mbaoma et al., 2025)
		Aedes atropalpus	American rock pool mosquito	Invasive species (Giunti et al., 2023)
		Anopheles arabiensis	Summer malaria mosquito	Vector of *Plasmodium* falciparum (malaria parasite) (Kweyamba et al., 2025)
		Anopheles coluzzii	African malaria mosquito	Vector of *Plasmodium* falciparum (Ahoua Alou et al., 2025)
		Anopheles gambiae	African malaria mosquito	Vector of *Plasmodium falciparum* (Kweyamba et al., 2025), *Wuchereria bancroft*i (parasite that causes lymphatic filariasis, or elephantiasis) (Reimer and Pryce, 2024)
		Culex pipiens	Common house mosquito	Vector of West Nile virus, St Louis encephalitis virus, Japanese encephalitis virus, Usutu virus (Tolsá-García et al., 2023)
		Culex quinquefasciatus	Southern house mosquito	Vector of West Nile virus, St Louis encephalitis virus (Tolsá-García et al., 2023)
		Anastrepha fraterculus	South American fruit fly	Agricultural pest (Vreysen et al., 2021)
		Anastrepha ludens	Mexican fruit fly	Agricultural pest (Vreysen et al., 2021)
		Bemisia tabaci	Cotton, Tobacco, Silverleaf, Sweet potato, or Silverleaf whitefly	Agricultural pest (Saurabh et al., 2021)
		Ceratitis capitata	Mediterranean fruit fly	Agricultural pest (Vreysen et al., 2021)
		Drosophila mauritiana	A species of fruit fly, vinegar fly	–
		Drosophila melanogaster	Common fruit fly, vinegar fly	–
		Drosophila migrospiracula	A species of fruit fly, vinegar fly	–
		Forcipomyia taiwana	Little black mosquito	Biting midge (sucks human blood) (Ching et al., 2024)
		Glossina spp. (including *G. austeni* and *G. morsitans*)	Tsetse flies	Vectors of African trypanosome species that cause Human African Trypanosomiasis (or African Sleeping Sickness) and Nagana (African animal trypanosomiasis) (Benoit et al., 2015)
		Hermetia illucens	Black soldier fly	Potential for bioconversion (Franco et al., 2025)
	Lepidoptera	*Bombyx mori*	Silkworm, silk moth	Producer of biomaterial with many applications (Khosropanah et al., 2025; Das et al., 2025)
		Heliconius charithonia	Zebra longwing butterfly, zebra heliconian	–
		Hyalophora cecropia	Cecropia moth, Cecropia silkmoth	–
		Maruca vitrata	Soybean pod borer	Agricultural pest (Srinivasan et al., 2021)
		Ostrinia scapulalis	Adzuki bean borer, adzuki bean worm	–
		Polygonia c-aureum	Asia comma	–
	Hymenoptera	*Apis mellifera*	Western honeybee, European honeybee	Producer of honey and secondary production derivates; key pollinator for many crops (Maggi and Mitton, 2025)
		Osmia bicornis	Red mason bee	Important pollinator (Zajdel et al., 2024)
		Asobara tabida	-	Parasitoid wasp (*Drosophila* larval hosts) (Prevost et al., 2005)

		Camponotus festinatus	A species of carpenter ant	–
		Temnothorax rugatulus	A species of ant	–
		Eupelmus vuilleti	A species of parasitoid wasp	–
	Dermaptera	*Opisthocosmia silvestris*	Earwig	–
	Neuroptera	*Chrysoperla nipponensis*	A species of green lacewing	–
	Phasmatodea	*Bacillus rossius*	European stick insect	–
	Siphonaptera	*Hystrichopsylla talpae*	Mole flea	–
Telotrophic meroistic	Coleoptera	*Coccinella septempunctata*	Common ladybug, seven-spotted ladybug	Biological control agent (Altaf et al., 2025)
		Harmonia axyridis	Harlequin, Asian, or multicolored lady beetle	Biological control agent (Camacho-Cervantes et al., 2021)
		Colaphellus bowringi	Cabbage beetle	–
		Creophilus maxillosus	Hairy rove beetle	Forensically useful (Wydra et al., 2024)
		Dytiscus marginalis	Great diving beetle	–
		Galeruca daurica	A species of leaf beetle	Agricultural pest (Li et al., 2024)
		Tenebrio molitor	Yellow mealworm beetle	Edible (Nachtigall et al., 2025)
		Tribolium castaneum	Red flour beetle	Storage pest (Ghada et al., 2025)
	Hemiptera	*Homalodisca vitripennis*	Glassy winged sharpshooter	Agricultural pest (Lessio and Alma, 2021)
		Nephotettix cincticeps	Rice green leafhopper	Agricultural pest (Kham et al., 2024)
		Perillus bioculatus	Two-spotted stink bug	Biological control agent (Hough-Goldstein and McPherson, 1996)
		Rhodnius prolixus	Kissing bug	Vector of *Trypanosoma cruzi* (Chagas disease parasite) (Lange et al., 2022)
		Riptortus pedestris	Bean bug	Agricultural pest (Hu et al., 2025)
		Kermes quercus	Striped kermes	European plant parasite (Podsiadło *et al.*, 2018)

[a] Common name for insects in the order Mecoptera.

Adult insect ovary anatomy

The insect female reproductive system includes a pair of ovaries, each connected to a main oviduct through a lateral oviduct, in addition to sperm storage organs, accessory glands, and a uterus (Klowden, 2013; Pascini and Martins, 2017; da Silva and Costa-Leonardo, 2025) (Fig. 1). Each ovary comprises multiple ovarioles that function as individual egg production lines. The number of ovarioles varies across insect species. For example, *D. melanogaster* have 15–20 ovarioles, while dung beetles have a single ovariole and queens of several eusocial insects can have over 500 ovarioles per ovary (Church *et al.*, 2021). In contrast to most dipterans, *Glossina* spp. have only two ovarioles per ovary and produce a single oocyte at a time (while the remaining ones remain arrested) from alternating ovaries, with each female producing 8 to 10 progeny during her lifetime. The secretions that support larval development in the expanded uterus are produced by a modified accessory gland composed of branched tubules and referred to as milk gland (Benoit *et al.*, 2015). Each insect ovariole consists of either an anterior germarium housing germ cell precursors or a tropharium (sometimes also called germarium) filled with interconnected trophocytes, followed by chronologically ordered developing oocytes closely associated with an epithelium of somatic follicle cells (Fig. 2) (Klowden, 2013). Depending on the germline composition and organization, ovarioles are classified as panoistic or meroistic (Klowden, 2013).

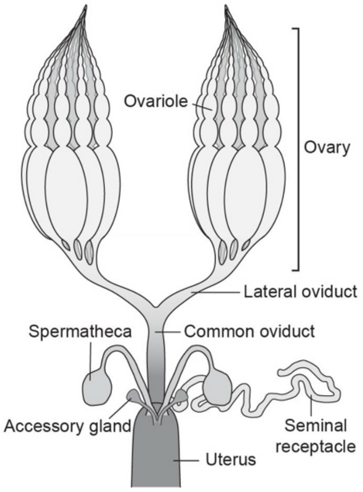

Fig. 1 ***D. melanogaster*** **reproductive tract.** Diagram showing a pair of *D. melanogaster* ovaries (composed of ovarioles), a pair of lateral oviducts, the common oviduct, a pair of spermathecae, the seminal receptable, a pair of accessory glands, and the uterus, with anterior to the top and posterior to the bottom. At the posterior end of each ovariole, mature oocytes are released into lateral oviducts, which join into the common oviduct. The spermathecae and seminal receptacle store sperm, which fertilize oocytes in the uterus. Secretions from the spermatheca and the accessory glands (or paraovaria) regulate ovulation.

Panoistic ovaries

In more ancestral panoistic ovarioles, germ cell progenitors (i.e., oogonia) only generate oocytes, such as in cockroaches, dragonflies, crickets, and praying mantids (Matsuzaki, 1971; Buning, 1993; Winnick, Holwell and Herberstein, 2009; Klowden, 2013). In the cockroach *Periplaneta americana* (Blattodea), each ovary consists of eight ovarioles subdivided into six zones (Fig. 2A) (Anderson, 1964). Zone I is the terminal filament, which is a stack of postmitotic somatic cells. Zone II is the germarium, housing oogonia, young oocytes and prefollicular cells (Fig. 3A). In zone III, oocytes are not linearly organized and begin envelopment by follicle cells. Zone IV is a large region composed of linearly organized oocytes with a complete monolayer of follicle cells at different developmental stages. Zone V comprises later developing oocytes filled with yolk granules (Fig. 2A), and Zone VI is the pedicel, a fine duct that connects with the lateral oviduct. This overall organization is similar in many panoistic ovarioles, although there are variations; for example, ovarioles in the scorpionfly *Nannochorista neotropica* (Mecoptera) lack a germarium (Simiczyjew, 2002).

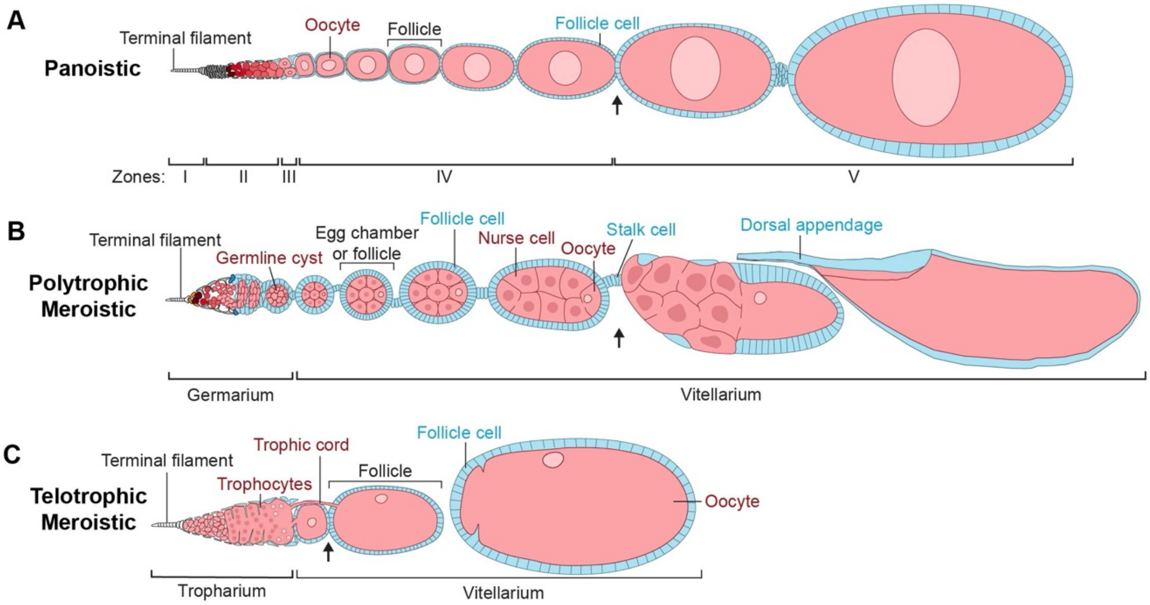

Fig. 2 **Examples of panoistic, polytrophic meroistic, and telotrophic meroistic ovarioles.** (A) Diagram of panoistic ovariole from a cockroach. Panoistic ovarioles do not have supporting nurse cells or trophocytes. In the cockroach *P. americana*, the ovariole is subdivided into six zones. Zone I is the terminal filament. Zone II is the germarium, housing oogonia, young oocytes and prefollicular cells. Zone III has oocytes that are not linearly organized and are being enveloped by follicle cells. Zone IV is a large region composed of linearly organized developing oocytes with a complete monolayer of follicle cells. Zone V has oocytes filled with yolk granules. Zone VI is the pedicel (not shown). (B) Diagram of polytrophic meroistic ovariole from the fruit fly *D. melanogaster*. The germarium houses germline stem cells and follicle stem cells that support the formation of egg chambers. Egg chambers consist of a 16-cell germline cyst (15 nurse cells and one oocyte, all interconnected through ring canals) surrounded by follicle cells and remain in chronological order as they progressively develop along the vitellarium. Egg chambers are separated from the germarium and each other by stalk cells. Nurse cells eventually dump their cytoplasmic contents into the oocyte and undergo programmed cell death. Follicle cells secrete the eggshell and form specialized structures such as the dorsal appendage. (C) Diagram of telotrophic meroistic ovariole from the kissing bug *R. prolixus*. The tropharium holds mitotic germ cells, trophocytes, and more posteriorly located prefollicular tissue and primary oocytes. Oocytes individually enveloped by follicle cells (follicles) are present in the vitellarium. While syncytial trophocytes remain in the tropharium, they remain attached to each individual developing oocyte by a trophic (or nutritive) cord, which is severed at the end of vitellogenesis. Anterior is to the left; arrow indicates the onset of vitellogenesis; the germline is shown in pink and follicle cells in blue.

Meroistic ovaries

In meroistic ovaries, germ cell precursors give rise to oocytes and supportive nurse cells (or trophocytes) (Klowden, 2013). Nurse cells become polyploid through endoreplication and they transfer RNAs, proteins, ribosomes, mitochondria, and other factors to support the growth and development of the oocytes as well as early embryogenesis. Meroistic ovaries can be further subdivided into polytrophic or telotrophic, depending on how oocytes and nurse cells or trophocytes are organized along ovarioles.

Polytrophic meroistic ovaries

Most holometabolous insects have polytrophic meroistic ovarioles (Klowden, 2013). In polytrophic meroistic ovarioles, the oocyte and nurse cells are clonally derived and remain interconnected through cytoplasmic bridges within egg chambers (also known as follicles) along the ovarioles. In the *D. melanogaster* ovary, each ovariole comprises an anterior germarium followed by the vitellarium, a string of successively organized egg chambers (Fig. 2B) (Spradling, 1993). The germarium is divided into three regions (Fig. 3B). Region 1 includes germline stem cells (GSCs) and their mitotically dividing daughters—cystoblasts and two-, four-, and eight-cell cysts—in addition to somatic terminal filament cells, cap cells, and inner germarium sheath (IGS) cells (also known as escort cells). Region 2 contains 16-cell germline cysts that are not yet completely enveloped by follicle cells, and it is further subdivided into 2a and 2b. In region 2a, 16-cell germline cysts are associated with IGS cells and have not yet organized into a single file. In region 2b, 16-cell cysts become lens-shaped and span the width of the germarium. Follicle stem cells (FSCs) located immediately anterior to the 2a/2b border generate early follicle cells (or pre-follicular cells) that begin to associate with the 16-cell cysts in 2b. Region 3 contains a round 16-cell cyst surrounded by follicle cells and is also referred to as a stage 1 egg chamber (or follicle) (Fig. 3B). Egg chambers in the vitellarium are separated from the germarium and each other by stalk cells—a subpopulation of follicle cells—and they continue to develop to form mature stage 14 oocytes that are ovulated, fertilized, and laid as eggs (Fig. 2B) (Spradling, 1993). In the silk moth *Bombyx mori* (Lepidoptera) ovary, which has four ovarioles, egg chambers contain one oocyte and seven nurse cells and develop through 12 morphologically distinct stages (Yamauchi and Yoshitake, 1984; Telfer, 2009), but early germline stages in the germarium have not been well studied. Activated ovaries of the honeybee queen *Apis mellifera* (Hymenoptera) have a germarium followed by oocytes (surrounded by follicle cells) attached to 31-nurse cell clusters (Torres, 1980; Aamidor *et al.*, 2022). In the ovariole of the hematophagous midge *Forcipomyia taiwana* (Diptera), a single nurse cell is connected to each oocyte (Midge *et al.*, 2020).

Telotrophic meroistic ovaries

Telotrophic meroistic ovaries are thought to have evolved from polytrophic meroistic ovaries and they occur in insects such as hemipterans, beetles, and mayflies (Büning, 2006; Klowden, 2013). In telotrophic meroistic ovarioles, the nurse cells (called trophocytes) remain in the tropharium and feed the oocytes through a nutritive (or trophic) cord as they develop along the ovariole. In the kissing bug *Rhodnius prolixus* (Hemiptera), each ovary has seven ovarioles. The ovarioles contain a terminal filament, tropharium, vitellarium, and pedicel (Fig. 2C). The tropharium has three regions, or zones (Fig. 3C). Zone 1 contains mitotically dividing germ cells. In zone 2, trophocytes (or nurse cells) form syncytia that interact with cytoplasmic extensions from peripheral cells and enter endoreplication. Zone 3 has degenerating trophocytes and prophase I arrested oocytes that accumulate posteriorly until oogenesis is activated (after a blood meal) and oocytes become surrounded by follicle cells and progress through the vitellarium (Fig. 2C) (Nunes-da-Fonseca *et al.*, 2017). In the red flour beetle *Tribolium castaneum* (Coleoptera), each ovary has five or six ovarioles. At the anterior of each ovariole, a terminal filament is followed by the tropharium, which contains non-proliferating germ cells (nurse cells; generated during late larval and pupal stages), posterior prefollicular cells, and 30 to 40 arrested oocytes (Trauner and Büning, 2007). In the posterior region of the tropharium, stage I primary oocytes are followed by stage 2 oocytes surrounded by prefollicular tissue. During stage 3, the larger oocyte is individually surrounded by follicle cells, marking the beginning of the vitellarium, where linearly arranged follicles progress through oogenesis. Yolk uptake occurs during stages 6 and 7, and eggshell secretion initiates at stage 8 (Parthasarathy *et al.*, 2010). Similar ovariole organization and lack of GSCs also occurs in other beetle species that have been examined (Büning, 2006).

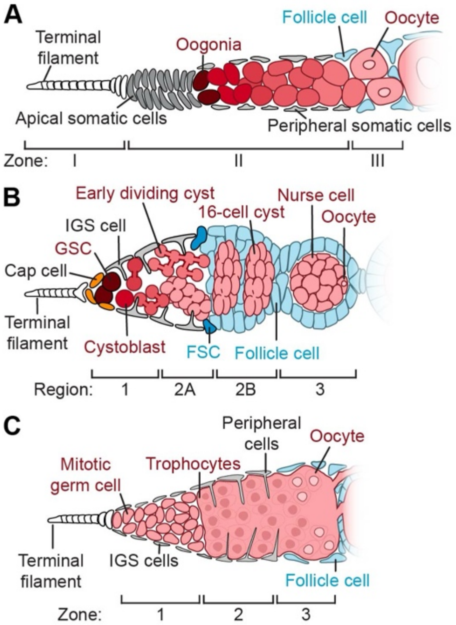

Fig. 3 **Germarium and tropharium examples.** (A) Diagram of anterior region of ovariole from a cockroach. The germarium corresponds to zone II and contains proliferating apical somatic cells and oogonia, young oocytes, and prefollicular cells. The terminal filament is termed zone I, while zone III has oocytes that are not linearly organized and are being enveloped by follicle cells. (B) Diagram of germarium from *D. melanogaster*. Two or three germline stem cells (GSCs) reside in a niche composed of cap cells, terminal filament cells, and a subset of inner germarial sheath (IGS) cells. GSCs divide asymmetrically to self-renew and give rise to a daughter cystoblast. The cystoblast undergoes four rounds of incomplete mitoses to form a 16-cell cyst, which is then surrounded by follicle cells produced by two follicle stem cells (FSCs). Region 1 includes GSCs, cystoblasts, and two-, four-, and eight-cell cysts in contact with IGS cells. Region 2a contains 16-cell germline cysts associated with IGS cells. Region 2b has lens-shaped 16-cell cysts spanning the width of the germarium beginning contact with follicle cells. Region 3 represents a round 16-cell germline cyst fully enveloped by follicle cells (known as stage 1 egg chamber) ready to bud off the germarium. (C) Diagram of a tropharium from *Rhodnius prolixus.* Zone 1 contains mitotically dividing germ cells. Zone 2 has syncytial trophocytes (or nurse cells) that interact with peripheral cell extensions and enter endoreplication. Zone 3 has degenerating trophocytes and prophase I arrested oocytes (generated during earlier developmental stages), and follicle cells. Oocytes remain in zone 3 until oogenesis is activated by a blood meal.

Major processes during adult insect oogenesis

During adult insect oogenesis, complex processes ensure the successful development of eggs from germ cell precursors over the course of hours to days. In *D. melanogaster*, oogenesis takes approximately 10 days, during which GSCs give rise to early proliferating daughters that, together with the progeny of FSCs will form egg chambers that develop, grow, and undergo vitellogenesis and maturation to form stage 14 oocytes. Mature oocytes are then ovulated, fertilized, and laid as eggs (Spradling, 1993). In other insects, similar events take place, although clear differences also exist.

Early germline development and egg chamber formation

In most cases, very early germline development within the germaria or tropharia (Fig. 3) of adult insects is not well described, although it appears that only some insect species may contain GSCs that continuously support oogenesis, while others have a pre-determined number of oocytes. The presence and type of germline cysts also vary widely depending on the type of ovariole.

Germline stem cells and germ cell precursors

In *D. melanogaster* females, lineage tracing experiments demonstrated that each germarium contains two or three GSCs (Margolis and Spradling, 1995). These GSCs reside in a specialized microenvironment (or niche) made up of cap cells, terminal filament cells, and a subset of IGS cells. Key factors required for GSC maintenance and function have been identified (Drummond-Barbosa, 2019; Hinnant *et al.*, 2020). For example, genetic mosaic analyses combined with overexpression experiments demonstrated that GSCs are maintained by a niche source of bone morphogenetic protein signals that directly stimulate GSCs (Xie and Spradling, 1998) and repress their premature differentiation (Chen and McKearin, 2003a, 2003b; Song *et al.*, 2004). GSCs also require E-cadherin-mediated adhesion to ensure their physical attachment to cap cells and thereby retention in the niche (Song and Xie, 2002). GSCs undergo asymmetric divisions perpendicular to the niche, such that one of the daughters remains within the niche as a renewed GSC, while the other daughter, arising outside of the niche, turns on expression of the differentiation factor Bam to become a cystoblast. The decision between GSC self-renewal and differentiation has been reviewed in detail elsewhere (Drummond-Barbosa, 2019; Kahney, Snedeker and Chen, 2019; Hinnant, Merkle and Ables, 2020). Morphological evidence suggests that GSCs are present in the ovaries of other insect species, including the polytrophic meroistic ovaries of the earwig *Opisthocosmia silvestris* (Dermaptera), which has a simplified niche lacking cap cells (Tworzydlo, Kloc and Bilinski, 2010), and the panoistic ovaries of *Blattella germanica* (Blattodea) (Rumbo, Pagone and Piulachs, 2023) and the firebrat *Thermobia domestica* (Zygentoma) (Tworzydlo *et al.*, 2014). GSCs are also presumed to exist in polytrophic meroistic ovaries of *B. mori* (Yamauchi and Yoshitake, 1984; Funaguma *et al.*, 2007; Carter *et al.*, 2013). In adult mosquito *Aedes aegypti* (Diptera) females, no terminal filament is present—they degenerate during pupal development—and it is unclear if active GSCs support oogenesis (Zhang *et al.*, 2023).

In contrast to most of the examples above, GSCs are thought to be generally absent from telotrophic meroistic ovaries, such as those in Neuroptera, Ephemeroptera (mayflies), Hemiptera, and Coleoptera (Büning, 2005, 2006). For example, in the rove beetle *Creophilus maxillosus* (Coleoptera), the formation and differentiation of nurse cells and oocytes occur during larval and pupal stages and, by eclosion, each adult ovariole has several chains of more than 12 interconnected nurse cells each linked to one posterior oocyte (Kloc, 2019). In the polytrophic meroistic ovarioles of the flea *Hystrichopsylla talpae* (Siphonaptera), no GSCs or other dividing germ cells are present (Büning and Sohst, 1988) and the panoistic ovarioles of the European stick insect *Bacillus rossius* (Phasmatodea) do not appear to contain GSCs either (Taddei *et al.*, 1993). Interestingly, a recent study in queens of *A. mellifera* showed that, although typical GSCs are absent from their polytrophic meroistic ovarioles, eight-cell germline clusters appear to divide and maintain a relatively constant pool of progenitors during adult reproductive life (Cullen *et al.*, 2023).

Early germline cysts

In the polytrophic meroistic ovarioles of *D. melanogaster*, the cystoblast undergoes four rounds of synchronous mitosis with incomplete cytokinesis to produce two-, four-, eight-, and 16-cell cysts interconnected by stable intercellular bridges, or ring canals. Newly formed 16-cell cysts undergo premeiotic S before entering meiotic prophase I. Although all 16 cells initiate meiosis, only the oocyte remains in meiosis and the 15 nurse cells undergo endoreplication (Spradling, 1993). The number of cystocyte divisions can vary in polytrophic meroistic ovaries. For example, in the cecropia moth *Hyalophora cecropia* (Lepidoptera) and in *Ae. aegypti*, eight-cell cysts are formed through three division rounds (Fiil, 1974; Telfer, 2009), while *A. mellifera* queens have 32-cell cysts (Torres, 1980; Aamidor *et al.*, 2022). A recent study showed that four molecularly distinct populations of IGS cells promote early germline differentiation by progressively controlling GSC maintenance, cyst formation, meiosis, and oocyte specification in *D. melanogaster* (Tu *et al.*, 2021).

In telotrophic meroistic ovaries, early germ cell proliferation to generate nurse cells and oocytes occurs in the germarium of larval and pupal ovarioles; in adult ovarioles, nurse cells (or trophocytes) remain in the tropharium and oocytes are present more posteriorly (Klowden, 2013). In Coleoptera, a large tropharium contains hundreds to thousands of nurse cells arranged in longitudinal rows of interconnected cells and embedded within a network of interstitial cells, with each nurse cell row connecting posteriorly with an oocyte (Büning, 1972, 2006; Trauner and Büning, 2007). Notably, adult *T. castaneum* female ovaries appear not to have germ cell proliferation, based on the absence of germ cells labeled with the mitosis marker phospho-histone H3 (Trauner and Büning, 2007). By contrast, in the adult ovarioles of the hemipteran *R. prolixus*, mitotically dividing germ cells are detected in zone 1 and are thought to renew the nurse cell population in zone 2, which degenerates in zone 3—although the number of oocytes is pre-determined during 5th instar nymph development (Nunes-da-Fonseca *et al.*, 2017).

Germline cysts are absent in panoistic ovarioles. Instead, oogonia proliferate in adult stages to directly generate oocytes, such as in the praying mantid *Ciulfina klassi* (Mantodea) (Winnick *et al.*, 2009), in the *P. americana* (Anderson, 1964) and in the bush cricket *Isophya nervosa* (Orthoptera) (Amutkan Mutlu and Suludere, 2022).

Fusome morphogenesis

In multiple insects—such as fruit flies, honeybees, wasps, moths, ponerine queenless ants, rove beetles, and diving beetles—the early germline contains a specialized actin-rich and vesicular organelle, the fusome (Büning, 2006; Okada *et al.*, 2010; Kloc, 2019; Hinnant *et al.*, 2020; Cullen *et al.*, 2023; Diegmiller *et al.*, 2023). In *D. melanogaster*, the fusome is required for cyst formation and oocyte specification (Lin, Yue and Spradling, 1994; Lin and Spradling, 1995) and its morphogenesis has been well described. The GSC and cystoblast both contain a round fusome (also called a spectrosome). In GSCs, the fusome is present in close juxtaposition to cap cells and changes shape during the cell cycle. In two-, four-, eight-, and 16-cell cysts, the fusome grows and becomes progressively more branched, interconnecting all cystocytes (De Cuevas and Spradling, 1998). Although many *D. melanogaster* fusome components have been identified (Lighthouse *et al.*, 2008) and the fusome has been shown to organize microtubules and localize key oocyte determinants (Grieder *et al.*, 2000; Nashchekin *et al.*, 2021), its molecular functions remain largely unknown.

Follicle stem cells and germline cyst encapsulation

Germline cyst encapsulation by follicle cells, as well as the FSCs that give rise to them, have been well studied in *D. melanogaster*. Elegant lineage tracing studies originally showed that each germarium contains two FSCs located immediately anterior to region 2a/2b border in the germarium (Margolis and Spradling, 1995), in agreement with multiple subsequent studies (Drummond-Barbosa and Spradling, 2001; LaFever and Drummond-Barbosa, 2005; Nystul and Spradling, 2007, 2010; LaFever *et al.*, 2010). Another study, using a novel clonal analysis system, proposed the existence of 14–16 FSCs organized in three rings in each germarium (Reilein *et al.*, 2017). However, a more recent study showed that the latter conclusion was incorrect—stemming from the use of a clonal marking system with a high rate of leaky clone production—and unequivocally demonstrated using multiple lineage tracing systems that only two FSCs are present in each germarium (Fadiga and Nystul, 2019). FSCs and their early differentiating progeny are highly regulated by many signaling pathways (Waghmare and Page-McCaw, 2018; Rust and Nystul, 2020). For example, follicle cell encapsulation of 16-cell germline cysts to form round stage 1 egg chambers (Fig. 3B) is primarily mediated by Delta-Notch signaling, which is also required later in oogenesis for the anterior-posterior polarization of the oocyte (Bender *et al.*, 1993; López-Schier and St. Johnston, 2001). Putative FSCs have also been identified in *T. castaneum* based on EdU incorporation and RNAi knockdown of a potential regulator (Teuscher *et al.*, 2017).

Egg chamber growth and development

Once outside of the germarium, egg chambers (or follicles) continue to develop in the vitellarium. The number of developing egg chambers can vary dramatically among ovarioles from different insect species, ranging from two or three in *Ae. aegypti* to hundreds in some Lepidopterans (Ullmann, 1973; Fiil, 1974; Telfer, 2009). The development of egg chambers has been morphologically described in multiple insects, including fruit flies, ants, and Lepidopterans, among others, and often has distinct pre-vitellogenic and vitellogenic phases.

Previtellogenic egg chamber development

Oocyte and nurse cell development

In *D. melanogaster*, egg chambers develop through 14 morphologically distinct stages to produce a mature oocyte, with vitellogenesis beginning at stage 8 (Spradling, 1993). As egg chambers grow and develop (until stage 10), nurse cells become highly polyploid through 10 to 12 rounds of endocycles, which are modified cell cycles that alternate G and S phases (Lilly and Spradling, 1996). In stages 2–5, the nurse cell DNA is polytene (i.e., sister chromatids remain closely aligned), creating five “blobs” of DNA per nuclei, corresponding to each of the major chromosome arms. During stage 6, sister chromatids separate, and the DNA becomes dispersed (Dej and Spradling, 1999). Polyploidy enables nurse cells to produce and transport large amounts of RNA, protein, ribosomes, organelles, and various other factors through ring canals into the oocyte to support its growth and, after fertilization, early embryo development. The oocyte itself remains arrested in prophase I through most of oogenesis and is largely transcriptionally inactive and its chromosomes are highly condensed into a karyosome within the oocyte nucleus (or germinal vesicle) (Spradling, 1993).

In telotrophic meroistic ovaries, trophocytes can become moderately polyploid to increase production of RNA, protein, and other macromolecules, which are transported to developing oocytes via microtubule-based anterior extensions of the oocyte called trophic cords (Ullmann, 1973; Büning, 2006; Kloc, 2019). However, the oocyte of the yellow mealworm beetle *Tenebrio molitor* (Coleoptera) is also capable of RNA synthesis (Ullmann, 1973). In panoistic ovaries, which lack trophocytes, the oocyte nucleus has been proposed to be responsible for the synthesis of all oocyte RNA. Accordingly, extrachromosomal rDNA amplification is generally observed in panoistic ovaries, which has been well described in the house cricket *Acheta domesticus* (Orthoptera) (Jaworska *et al.*, 1973; Ware *et al.*, 1987). In addition, lampbrush-like chromosomes have been observed in migratory locusts, grasshoppers, house crickets, and cockroaches (Bogolyubov and Parfenov, 2008). However, rDNA amplification does not appear to occur in the panoistic ovarioles of *B. germanica* (Cave, 1976) while, conversely, rDNA amplification has been documented in some insects with telotrophic meroistic ovaries, such as the dytiscid beetle *Dytiscus marginalis* (Coleoptera) and *C. maxillosus* (Gall and Rochaix, 1974; Kloc, 2019).

Follicle cell events

The behavior of follicle cells is well described in *D. melanogaster* egg chamber development. For example, in stage 1 through 8 egg chambers, follicle cells are cuboidal and form an even epithelium around the developing germline cyst, and they continuously proliferate through stage 6. During stage 7, follicle cells exit their mitotic program and initiate endoreplication. Different types of differentiated follicle cells play important roles in egg chamber development. For example, stalk cells separate each egg chamber from the germarium and each other, while polar cells contribute to egg chamber polarization (Rust and Nystul, 2020). Interestingly, follicle cells deposit a corset-like polarized extracellular matrix soon after egg chamber formation. The follicular epithelium undergoes circumferential movement along this matrix, causing the entire egg chamber to rotate perpendicularly to the anterior-posterior axis and driving egg chamber elongation (Horne-Badovinac, 2014; St Johnston, 2023).

Vitellogenic egg chamber development

Vitellogenesis

Vitellogenic egg chambers are marked by the presence of yolk, composed of proteins, lipids, and glycogen, in the oocyte. In virtually all insects, yolk proteins (or vitellogenins) are synthesized mainly by the fat body—an organ composed of adipocytes and liver-like oenocytes (Arrese and Soulages, 2010; Li *et al.*, 2019)—and transported through the hemolymph for uptake by the oocyte. A transient separation of follicle cell junctions (i.e., patency) allows yolk proteins to access and be taken up by the oocyte (Parthasarathy *et al.*, 2010; Santos *et al.*, 2011). Follicle cells also produce yolk proteins in a few insects, including *D. melanogaster*, *R. prolixus*, and *Hyalophora* silk moths (Brennan *et al.*, 1982; Telfer, 2009; Nunes-da-Fonseca *et al.*, 2017). Vitellogenin production has also been reported in nurse cells and hemocytes in some insect species (Wu *et al.*, 2021; Kodrik *et al.*, 2023). In lepidopterans, pupal storage hexamerins incorporated into the adult fat body contribute amino acids for yolk protein production (Telfer, 2009). A recent study in *D. melanogaster* showed that larval fat body hexamerins (LSP1α, LSP2, FBP1, and FBP2) regulate amino acid availability to limit larval growth and ensure proper growth of tissues that form adult structures (i.e., imaginal discs) (Valzania *et al.*, 2024). These storage proteins are also required for pupal development and adult fitness, including male and female fertility (Valzania *et al.*, 2024). However, the severe developmental defects caused by knock down of hexamerins (Valzania *et al.*, 2024) preclude any conclusion about whether or not hexamerins directly support yolk production or any aspect of adult *D. melanogaster* oogenesis. In *D. melanogaster*, the uptake of yolk proteins (YP1, YP2, and YP3) requires the vitellogenin receptor encoded by the gene *yolkless* (Schonbaum *et al.*, 2000). Interestingly, *Glossina* has a single yolk protein gene orthologous to YP2, and yolk protein is only produced by follicle cells surrounding the developing oocyte (Benoit *et al.*, 2015). Similar to *D. melanogaster*, systemic RNAi of the *yolkless* homolog in cockroaches prevents yolk uptake by oocytes in their panoistic ovarioles (Ciudad *et al.*, 2006). In the telotrophic meroistic ovaries of *R. prolixus*, RNAi-mediated knockdown of *Vg1* and *Vg2*, which encode vitellogenins, leads to the production of yolk-depleted eggs that fail to support embryogenesis (Pereira *et al.*, 2025). In *D. melanogaster*, the oocyte takes up large amounts of yolk proteins in stages 8 through 10 egg chambers (Cummings and King, 1969; Spradling, 1993). During stage 10, the oocyte accumulates high levels of neutral lipid stores composed of triglycerides and sterols (Parra-Peralbo and Culi, 2011; Sieber and Spradling, 2015). In the gut, diacylglycerols carrying dietary and *de novo*-synthesized fatty acids, along with sterols, are transferred to the apoB-family lipoprotein Lipophorin (Lpp), which is a major hemolymph lipid carrier (Palm *et al.*, 2012). Neutral lipid uptake requires Lpp receptors encoded by *lpr1* and *lpr2* in the germline and fat body-derived Lpp (Parra-Peralbo and Culi, 2011; Matsuoka *et al.*, 2017). During stages 12 to 14, glycogen accumulates in oocytes as mitochondrial metabolism shifts into respiratory quiescence (Sieber *et al.*, 2016). By contrast, in *B. mori*, lipid droplets and glycogen begin accumulating in the oocyte as soon as the egg chamber forms, while yolk proteins accumulate later (Yamauchi and Yoshitake, 1984). Similar to *D. melanogaster*, the tsetse fly *Glossina morsitans* (Diptera) expresses lipophorin in the adult fat body. RNAi knockdown of lipophorin reduces lipid levels in the hemolymph and delays oocyte development (Benoit *et al.*, 2011). In *R. prolixus*, a single vitellogenic oocyte (surrounded by binucleated follicle cells) is present at a time in each of its telotrophic ovarioles (Lange *et al.*, 2022).

Nurse cell dumping and oocyte meiotic maturation

During stage 11 of *D. melanogaster* oogenesis, nurse cells rapidly transfer their cytoplasmic content through ring canals to the oocytes in a process called dumping that requires actomyosin contraction. Actin bundles anchor the polyploid nurse cell nuclei in place, such that at stage 12 the oocyte occupies almost the entirety of the egg chamber but nurse cell nuclei surrounded by plasma membrane still remain at its very anterior (Buszczak and Cooley, 2000). Nurse cell remnants (closely associated with stretch follicle cells) are eliminated during stage 13 through a unique developmental cell death process (Lebo and McCall, 2021; Ghosh *et al.*, 2025). A recent study proposed that two of the nurse cell nuclei are transferred into the oocyte during stage 10B (through membrane fusion) prior to dumping and degraded within the oocyte (Ali-Murthy *et al.*, 2021). Dumping is also observed in other polytrophic meroistic ovarioles—e.g., it occurs at stages 6 and 7 during *B. mori* oogenesis (Yamauchi and Yoshitake, 1984) and in stage 7 of *A. mellifera* ovarioles (Aamidor *et al.*, 2022). In telotrophic ovarioles, the nutritive cord that connects nurse cells in the tropharium to growing oocytes is severed at the end of vitellogenesis before eggshell (also known as chorion) formation (Woodruff and Anderson, 1984). Meiotic maturation takes place in mid-to-late stage 13 oocytes in *D. melanogaster* (Von Stetina *et al.*, 2008), resulting in a final stage 14 oocyte ready to be ovulated, activated, fertilized and laid (Berg *et al.*, 2024).

Follicle cells and eggshell formation

In *D. melanogaster*, follicle cells perform different morphogenetic movements that contribute to the final shape and structures of the eggshell (Spradling, 1993; Duhart *et al.*, 2017). The follicle cell epithelial monolayer undergoes a major rearrangement during stage 9, such that by stage 10A, ~10% of follicle cells become squamous and thinly stretched over nurse cells in the anterior half of the egg chamber, while 90% of follicle cells become columnar (and taller on the dorsal side) and overlie the oocyte in the posterior half of the egg chamber. Also during stage 9, six to 10 border cells—a subset of anterior follicle cells—migrate through the nurse cells, reaching the border with the oocyte at the onset of stage 10A. During stage 10B, another group of 30 to 40 follicle cells migrates centripetally to cover the anterior pole of the oocyte, while a subset of dorsal follicle cells initiates dorsal appendage morphogenesis. Concomitant with these morphogenetic events, follicle cells also undergo modified cell cycles. Once follicle cells stop proliferating mitotically (stage 7), they undergo six to eight endocycles through stage 10A. Starting in stage 10B, follicle cells undergo chorion gene amplification to further support eggshell production (Calvi *et al.*, 1998). In telotrophic meroistic ovarioles, follicle cells also endoreplicate their DNA to increase RNA and protein production (Ullmann, 1973; Kloc, 2019). In the telotrophic meroistic ovaries of *T. molitor*, follicle cells are initially mitotic and form a columnar monolayer around the oocyte. During early vitellogenesis, follicle cells are polyploid and become cuboidal as patency begins, reaching maximal level during mid-vitellogenesis. In late vitellogenesis, follicle cells flatten and lose patency, as they start secreting the eggshell (Ullmann, 1973). In the panoistic ovarioles of the bush cricket *I. nervosa*, follicle cells surrounding the developing oocyte are cuboidal and form a monolayer, but as oogenesis progresses, follicle cells become columnar and tightly packed, forming a thicker layer around the maturing oocyte (Amutkan Mutlu and Suludere, 2022).

During the final stages of insect oogenesis, follicle cells secrete a complex extracellular matrix that makes up the eggshell. Holometabolous insect eggshells have an inner vitelline membrane and several chorionic layers, including the wax layer, the innermost chorionic layer, the endochorion (which contains air passages) and the exochorion (Cohen and Moussian, 2016). In *D. melanogaster*, the vitelline membrane is formed first (stage 10B), followed by the wax layer (stage 11), the innermost chorionic layer and endochorion (stages 11 to 14), and the exochorion (stage 14) (Cohen and Moussian, 2016). The endochorion air channels open to the outside through a few posteriorly located small aeropyles, the dorsal respiratory horns, and dorsal appendages (Spradling, 1993). Dorsal appendages are major structures formed through elaborate morphogenetic movements by a subset of follicle cells starting with the adoption of a slightly elongated shape in stage 10B, followed by onset of tube formation in stage 11, and tube elongation and remodeling during stages 12 and 13, as eggshell components are secreted (Berg, 2005; Horne-Badovinac, 2014; Duhart *et al.*, 2017). Follicle cells also form other specialized eggshell structures, including the micropyle (where the sperm enters) and the operculum (where the larva exits). Centripetal cells form the operculum and the outer micropyle anteriorly, and border cells build the canal inside the micropyle (Duhart *et al.*, 2017). The exochorion structures have varied patterns across insect species or even within the same species depending on the season (Cohen and Moussian, 2016; Donoughe, 2022). For example, many species lack dorsal appendages, and certain lepidopteran species can have up to 400 aeropyles per egg. Conversely, aeropyles are not detected in the eggs of some coleopterans such as *T. castaneum*. The eggs of some aquatic insect species develop a gill-like network that maximizes the air–water interface, and the dragonfly eggshell contains eight to 12 micropyles in the micropyle region and aeropyles are present throughout the eggshell (Cohen and Moussian, 2016).

Regulation of adult insect oogenesis by diet and other environmental factors

Insects invest enormous amounts of energy and resources into oogenesis, and their evolutionary success reflects their remarkable ability to minimize wasting these investments by tightly regulating egg production according to environmental and physiological conditions.

Diet

The availability of nutrients has a drastic effect on insect oogenesis (Wheeler, 1996). For example, fluctuation in food quality or availability leads to changes in oogenesis in synovigenic insects (i.e., those that produce eggs continuously through adult life) such as the tephritid flies *Anastrepha ludens* and *Anastrepha fraterculus* (Diptera), the twospotted stink bug *Perillus bioculatus* (Hemiptera), the glassy winged sharpshooter *Homalodisca vitripennis* (Hemiptera), and the field cricket *Gryllus lineaticeps* (Orthoptera), among others (Adams *et al*., 2002; Aluja *et al*., 2011; Goane *et al*., 2019; Treidel *et al*., 2021; Sisterson and Brent, 2022). In many crop-pollinating dipteran species, females feed on protein sources (e.g., other insects, eggs, food waste, feces) to stimulate oogenesis, as opposed to males, which only feed on pollen and nectar (Davis *et al*., 2023). Interestingly, sap-sucking insects rely on extracellular or intracellular symbionts that provide essential amino acids lacking from their diet (Hansen and Moran, 2011; Feng *et al*., 2019; Reis *et al*., 2020; Moriyama and Fukatsu, 2022) and are presumably important for oogenesis.

In *D. melanogaster*, egg production drops 60-fold when the flies are switched from a yeast-rich to a yeast-free diet (Drummond-Barbosa and Spradling, 2001). This drastic reduction in the rate of oogenesis is the combined result of changes in many oogenesis processes in previtellogenic and vitellogenic stages that lead to much smaller ovaries. On a yeast-rich diet, GSCs, early dividing cysts, FSCs and follicle cells have robust proliferation rates, and egg chambers grow, develop, and undergo vitellogenesis at similarly high rates to maintain continuous egg production (Drummond-Barbosa and Spradling, 2001). On a yeast-free diet, GSCs are not well maintained within their niches, proliferation rates drop by two- to three-fold, early germline cysts die at a high frequency in the germarium, and egg chambers grow more slowly, with most degenerating during early vitellogenic stages (Drummond-Barbosa and Spradling, 2001; Hsu and Drummond-Barbosa, 2009). In addition, nutrient starvation leads to changes in the subcellular localization of many proteins (Shimada *et al*., 2011; Hsu and Drummond-Barbosa, 2017), including the formation of large processing (P) bodies containing components of ribonucleoprotein complexes important for oogenesis in nurse cells (Shimada *et al*., 2011). Most of these changes occur within less than 18 h of switching diets (Drummond-Barbosa and Spradling, 2001), and the fewer eggs produced on a poor diet are of similar quality as those on a rich diet (Burn *et al*., 2015). Several groups have reported that a high sugar diet also decreases *D. melanogaster* fertility (Morris *et al*., 2012; Brookheart *et al*., 2017; Nunes and Drummond-Barbosa, 2023; Huang *et al*., 2024), primarily owing to increased death of early germline cysts and degeneration of vitellogenic follicles (Nunes and Drummond-Barbosa, 2023; Huang *et al*., 2024).

Other insects have similar responses to diet. In starved *T. castaneum* beetles, vitellogenin mRNA is absent and primary oocytes are only able to develop to stage 4. Upon feeding, vitellogenin mRNA levels increase and oocytes progress to stage 5 (Parthasarathy and Palli, 2011). *A. mellifera* honeybee queens prevented from feeding normally have fewer early germline progenitors, abnormal nurse cell dumping, and degeneration of early and late stage oocytes, resulting in smaller ovary size (Aamidor *et al*., 2022). Similarly, queen ants *Temnothorax rugatulus* (Hymenoptera) have fewer developing oocytes when their access to food is restricted (Negroni *et al*., 2021).

Hematophagous insects such as mosquitoes, fleas, and kissing bugs feed on sporadic large blood meals that stimulate oogenesis (Hastriter and Whiting, 2009; Gondim *et al*., 2018). Most adult mosquito females are anautogenous, requiring at least one blood meal from a vertebrate host for each clutch of 80 to 120 eggs to be produced (Valzania *et al*., 2019). In *Ae. aegypti*, arrested pre-vitellogenic primary egg chambers undergo little (if any) DNA replication; however, within two hours of blood feeding, follicle cells start proliferating mitotically and nurse cells undergo endoreplication, and cytoophidia—large filaments of active CTP synthase—appear in both cell types, marking the onset of vitellogenesis (Fiil, 1974; Valzania *et al*., 2019). [Incidentally, cytoophidia are also present in nurse cells and follicle cells in *D. melanogaster*, where they support endoreplication and follicular epithelium integrity, respectively (Wang *et al*., 2015, 2022)]. In another mosquito species, *Culex pipiens pallens* (Diptera), 200 follicles synchronously start developing 1 day after blood feeding, but then about 130 of them die by 3 days after feeding (Uchida *et al*., 2004). The number of eggs laid per clutch in mosquitos is proportional to the volume of blood ingested and protein is the main macronutrient for oogenesis (Harrison *et al*., 2022). Interestingly, a recent study using fractionated blood from different mammalian (human, rat) and avian (turkey, chicken) hosts to feed mosquitos showed that both the host source of blood or plasma and the type of plasma-derived protein (i.e., serum albumin, fibrinogen, and globulins) differ in their ability to stimulate oogenesis depending on the specific anautogenous mosquito species, namely *Ae. aegypti*, *Anopheles gambiae* and *Culex quinquefasciatus* (Diptera) (Harrison *et al.*, 2021). Other mosquito species are autogenous, in that females do not require a blood meal to mature the first egg batch, using instead resources from larval stores. For example, the American rock pool mosquito *Aedes atropalpus* (Diptera) is an obligatory autogenous for its first egg cycle; if they are not well fed as larvae, they produce fewer eggs in their first egg batch and require a blood meal before producing a second egg batch (Telang and Wells, 2004). In *R. prolixus*, meiosis I arrested oocytes initially accumulate in the posterior region of the tropharium; once the female has a blood meal, the oocytes gradually migrate posteriorly and follicle cells become highly proliferative to surround the oocytes (Nunes-da-Fonseca *et al.*, 2017). Multiple studies have investigated lipid metabolism following a blood meal and its connection with oogenesis in *R. prolixus* (Entringer *et al.*, 2021; Saraiva *et al.*, 2021; Silva-Oliveira *et al.*, 2021; Aredes *et al.*, 2022; Moraes *et al.*, 2022; Braz *et al.*, 2023). Remarkably, *R. prolixus* females must gorge the equivalent of up to two or three times their own body weight to ensure maximum egg production (Lange *et al.*, 2022).

Glossina tsetse flies are strict hematophagous and, despite producing few progeny, their adenotrophic viviparity generates a large demand for nutrients required to produce the milk that supports intrauterine larval growth—which involves over 100-fold increase in dry mass over 6 days—before larviposition. In newly eclosed females, development of the first oocyte begins in the right ovary with ovulation (and fertilization) occurring ~10 days later. Following ovulation, the second oocyte begins developing in the left ovary and completes maturation ahead of the female giving birth to its first larva, which is ready to pupariate. The second oocyte ovulates shortly after larviposition, and the cycle continues (Benoit *et al.*, 2015). Milk production and accompanying physiological changes are also cyclical. During embryonic development, the maternal fat body accumulates lipids (non-lactation or dry phase). The lipids are later mobilized to the milk gland along with amino acids and additional lipids obtained through blood meals to support milk production during larval growth (lactation phase). Without this intensive maternal transfer of nutrients, larvae are unable to develop (Benoit *et al.*, 2015). However, much remains unknown about how oocyte development itself is regulated by dietary inputs in *Glossina*.

Temperature

Temperature, a critical factor amid the current climate crisis (Voosen, 2025), influences insect egg production. In the tabanids family, which includes horse flies and deer flies, the time between a blood meal and egg laying increases with higher temperatures (Roberts, 1980). *Ae. aegypti* eggs only hatch successfully when blood-fed females are exposed to 12 to 32°C (Briegel *et al.*, 2003). In *A. gambiae* reared at 27°C, 30°C, or 32°C, blood feeding propensity, blood meal size, egg production, and hatching rates decrease progressively with the increase in temperature, and females are sterile at 32°C (Martin *et al.*, 2025). Prolonged exposure of *Glossina* flies to temperatures above 37°C can eliminate symbionts and decrease fertility (Benoit *et al.*, 2025); however, the specific effects of temperature on their obligate symbiont *Wigglesworthia* (see below) or on oogenesis have not been well studied. The reproduction of female aphids is a very interesting example: they are sexual and oviparous or asexual and viviparous depending on temperature and photoperiod (Tagu *et al.*, 2005).

Many studies have examined the effect of temperature in *Drosophila*. Multiple *Drosophila* species that undergo development at elevated temperatures have decreased fertility later as adults (Northrop, 1920; Plough and Strauss, 1923; Alpatov, 1932; Dobzhansky, 1935), and short exposures of adult females to extreme high temperatures causes vitellogenic egg chamber death and accumulation of mature oocytes (Gruntenko *et al.*, 2003). A more recent study showed that *D. melanogaster* females chronically exposed to suboptimal temperatures exclusively as adults also have reduced egg production. Exposure to a warm temperature of 29°C—warmer than the ideal 25°C—increases germline cyst death and vitellogenic egg chamber degeneration and reduces oocyte quality, while exposure to 18°C slows egg chamber growth despite improving GSC maintenance, early cyst survival, and oocyte quality (Gandara and Drummond-Barbosa, 2022).

More extreme lower temperatures induce adult diapause (or dormancy) in multiple insect species, including the nymphalid butterfly *Polygonia c-aureum* (Lepidoptera), the adzuki bean borer *Ostrinia scapulalis* (Lepidoptera), the mosquito *C. pipiens,* the Asian lady beetle *Harmonia axyridis* (Coleoptera), and the grasshopper *Stenocatantops splendens* (Orthoptera) (Saunders *et al.*, 1989; Meuti *et al.*, 2024). Some insects remain active but undergo reproductive diapause, such as monarch butterflies and several species of grasshopper and dipterans (Good and Tatar, 2001). In *D. melanogaster*, ovarian diapause can be induced in newly eclosed females exposed to short days at 10°C to 12°C, lasting up to 6 or 7 weeks (Saunders *et al.*, 1989). During reproductive diapause, vitellogenic egg chambers are largely missing but are again produced after females are transferred back to higher temperatures (Saunders *et al.*, 1989; Easwaran *et al.*, 2022; Hara and Yamamoto, 2022). A recent study showed that during reproductive diapause, there is also reduced niche signaling and GSCs divide less, show signs of DNA damage, and have altered morphology, all of which is reversed after recovery from a six-week diapause (Easwaran *et al.*, 2022).

Mating

The seminal fluid transferred during mating stimulates oogenesis in many insects (Chapman, 2001; Drummond-Barbosa, 2019; White *et al.*, 2021; Lange *et al.*, 2022). In *D. melanogaster*, egg laying increases rapidly within the first 18 h after mating (Heifetz *et al.*, 2001) and stays elevated for about ~10 days (Moshitzky *et al.*, 1996), and both sperm and male accessory gland proteins (Acps) promote faster vitellogenic egg chamber development (Heifetz *et al.*, 2001). *D. melanogaster* encodes ~80 Acps, and sex peptide (Acp70A) is sufficient to increase egg production for one or 2 days when provided to virgin females (Soller *et al.*, 1997; Chapman, 2001). Mating and sex peptide have also been reported to transiently increase GSC number and proliferation (Ameku and Niwa, 2016; Ameku *et al.*, 2018; Yoshinari *et al.*, 2020). Interestingly, the nucleic acids in the ovaries of *D. melanogaster* and *Drosophila migrospiracula* (Diptera) incorporate phosphorus derived from the male ejaculate, suggesting that mating can also help insect females meet the high demand for phosphorus used to produce large amounts of nucleic acids during oogenesis (Markow *et al.*, 2001). In the tsetse fly *Glossina austeni* (Diptera), mating increases blood meal size, stimulates oocyte development, and is required for ovulation (Ejezie and Davey, 1977). Similarly, fed *R. prolixus* virgin females only lay 70% as many eggs as fed mated females, and vitellogenic egg chambers accumulate in their ovarioles (Lange *et al.*, 2022). In honeybee queens, the vitellarium does not develop at all until after mating, when ovarioles grow in size as oocytes start undergoing vitellogenesis (Kocher *et al.*, 2008). Conversely, mating does not influence egg production in the Mediterranean fly *Ceratitis capitata* (Diptera) (Chapman *et al.*, 1998) or in the solitary bee *Osmia bicornis* (Hymenoptera) (Van Eeckhoven and Duncan, 2020).

Microorganisms

Interactions with various microorganisms also influence oogenesis in multiple insect species and have been extensively reviewed (Douglas, 2009; Drummond-Barbosa, 2019; Singh *et al.*, 2021; Stapleton *et al.*, 2022; Chabanol and Gendrin, 2024; Holt *et al.*, 2024; Lukasik and Kolasa, 2024; S. Zhang *et al.*, 2025). Intracellular bacteria *Wolbachia* are primarily vertically transmitted and occur in almost half of all insect species, affecting their reproduction through various mechanisms (Porter and Sullivan, 2023; Hyder *et al.*, 2024). For example, *Drosophila mauritiana* (Diptera) infected with *Wolbachia* have elevated GSC proliferation, decreased early germline death, and increased egg production compared to uninfected counterparts (Fast *et al.*, 2011), and multiple studies in *D. melanogaster* have examined various mechanisms through which *Wolbachia* manipulates oogenesis (Russell *et al.*, 2023; Serbus *et al.*, 2008; Drummond-Barbosa, 2019). In a study examining 13 populations of the parasitic wasp *Asobara tabida* (Hymenoptera), all individuals were infected by *Wolbachia*, and antibiotic treatment resulted in a lack of oocytes in the vitellarium and female sterility, suggesting that *Wolbachia* has become an obligatory symbiont in these populations (Dedeine *et al.*, 2001).

Other intracellular microorganisms influence oogenesis as well. *Anopheles arabiensis* (Diptera) mosquitos naturally harbor intracellular *Microsporidia MB* symbionts, which prevent mosquito infection with *Plasmodium* parasites that cause malaria and are vertically transmitted through GSCs, replicating in close coordination with oocyte development (Herren *et al.*, 2020; Onchuru *et al.*, 2024); however, the effect of *Microsporidia MB* on fertility is unclear. *Ae. aegypti* mosquitoes infected with the dengue virus DENV-2 have altered ovarian expression of many metabolic genes and reduced egg production (Feitosa-Suntheimer *et al.*, 2022). Interestingly, in the rice leafhopper *Nephotettix cincticeps* (Hemiptera), about 20% of vitellogenins are taken up by the oocyte independently of the vitellogenin receptor through a process requiring vitellogenin entry into the cytoplasm of an obligate intracellular bacterial symbiont, *Nasuia deltocephalinicola*, through a specific interaction between vitellogenin and *Nasuia* porin. Blocking this interaction with anti-porin antibodies significantly reduced later egg hatching, showing its importance for optimal embryonic development (Mao *et al.*, 2020). Middle East-Asia Minor 1 whitefly *Bemisia tabaci* (Diptera) adult females that feed on tobacco plants that are infected with the tomato yellow leaf curl China virus have increased vitellogenesis compared to those feeding on uninfected plants, although the underlying mechanisms are unknown (Guo *et al.*, 2012). Many plant sap-sucking hemipterans, such as scale insects (e.g., aphids, psyllids, and white-flies), house either obligate symbiotic bacteria or yeast-like symbionts, which are thought to play important roles in supplementing their diet with specific amino acids, sterols, and vitamins (Douglas, 2009). *Glossina* feed exclusively on blood—unlike mosquitos, which also feed on nectar—and require the obligate mutualistic symbiotic bacteria *Wigglesworthia glossinidia* as a source of B-vitamins and other co-factors for fertility (Attardo *et al.*, 2020). *W. glossinidia* reside in giant bacteriocyte cells within the bacteriome, a structure surrounding the dorsal midgut; however, morphologically distinct extracellular forms of these bacteria reside near the lumen of milk gland tubules, presumably to facilitate vertical transmission (Attardo *et al.*, 2020). More recently, yeast-like microorganisms were found exclusively in the fat body only during nymph and adult female feeding stages in the European plant parasite *Kermes quercus*, although their nutritional role has not been examined (Podsiadło *et al.*, 2018).

Extracellular microorganisms also affect insect oogenesis. For example, in *Ae. aegypti*, midgut bacteria contribute to blood digestion and egg production (Gaio *et al.*, 2011), and mating-induced changes in the midgut microbiome increase female fecundity (Taracena-Agarwal *et al.*, 2024). *Ae. aegypti* can also carry the trypanosomatid *Strigomonas culicis*, which disrupts egg laying and hatching rates (Bombaça *et al.*, 2021). Similarly, the fertility of *R. prolixus* is reduced by infection with *Trypanosoma rangeli* or *Trypanosoma cruzi* protozoans (Fellet *et al.*, 2014; Duarte Da Silva and Guarneri, 2023). Some insect species house a large number of gut microbes that may contribute to food utilization, such as the cricket *A. domesticus* and the black soldier fly *Hermetia illucens* (Diptera) (Jordan and Tomberlin, 2021), although the effects of these microorganisms on oogenesis have not been well studied. Queen honeybees have gut microbiota distinct from worker bees, partly because of their different diets; however, the effect of the microbiota on their reproduction is also unclear (Zumkhawala-Cook *et al.*, 2024). A recent study reported that the microbe *Acetobacter pomorum* promotes GSC proliferation and vitellogenic egg chamber development when environmentally provided to adult *D. melanogaster* females (Suyama *et al.*, 2023).

Other inputs

Social interactions

In some types of insects, including ants, bees, and wasps, social interactions can exert significant control on oogenesis (Cridge *et al.*, 2017; Kapheim, 2017; Luna-Lucena *et al.*, 2018; Knapp *et al.*, 2022). For example, genetically identical queen and worker *A. mellifera* honeybees have drastically different adult ovarian morphology and reproductive capacity—with queens laying thousands of eggs and workers being sterile—owing to developmental differences driven by extensive interactions between these castes. Worker bees produce and feed royal jelly to developing future queens. This worker-provided royal jelly diet promotes development of all ~200 ovariole primordia in future queens, which in developing workers undergo massive degeneration instead. Conversely, adult queens actively suppress activation of ovarian development in workers via pheromones, including the queen mandibular pheromone (QMP), that induce early oocyte death; in the absence of the queen, workers become fertile (Cridge *et al.*, 2017). Interestingly, exposure of *D. melanogaster* to QMP induces a starvation-like response that includes reduced ovarian insulin signaling and fertility, suggesting a possible evolutionary connection between QMP and diet-response mechanisms (Lovegrove *et al.*, 2023). In the ant *Camponotus festinatus* (Hymenoptera), the presence of a queen represses vitellogenin production in workers (Martinez and Wheeler, 1991). Intriguingly, a recent study reported that the presence of other flies blocks the inhibitory effects of light on *D. melanogaster* egg laying (Bailly *et al.*, 2023).

Olfactory and visual inputs

Recent studies suggest that olfactory cues contribute to the control of insect oogenesis. Mosquito *Ae. aegypti* females mutant for *orco*, which encodes the evolutionarily conserved odorant receptor co-receptor, lay a normal number of eggs of lower quality—i.e., the resulting embryos have developmental abnormalities—following the second blood meal (David *et al.*, 2023). Another study suggested that visual and olfactory inputs from the pupal parasitoid wasp *Pachycrepoideus sp*. promote GSC proliferation and increase egg production in *D. melanogaster* (Sadanandappa and Bosco, 2024). The potential roles of olfactory, visual, and other sensory cues in insect oogenesis remain largely unexplored.

Physiological signaling modulating oogenesis

Multiple physiological signals modulate oogenesis and mediate the response to various environmental factors, including diet-dependent signaling, hormones, neuropeptides, and other factors mediating inter-organ communication.

Insulin signaling, Venus kinase receptor, TOR, and AMPK

Insulin signaling, Venus kinase receptor, and TOR

In insects, insulin-like peptides (ILPs) are produced by medial neurosecretory cells in the brain (and in additional tissues) in response to nutrients and other stimuli, and they act through insulin receptors to control many physiological processes, including oogenesis (Antonova *et al.*, 2012; Drummond-Barbosa, 2019; Chowański *et al.*, 2021; Semaniuk *et al.*, 2021; Knapp *et al.*, 2022). In *D. melanogaster*, brain ILPs act directly on the germline to promote GSC proliferation, egg chamber growth, and vitellogenesis in response to diet, as shown through experiments involving genetic mosaic analysis, ablation of ILP-producing cells, and ovary transplantation (Fig. 4) (LaFever and Drummond-Barbosa, 2005; Richard *et al.*, 2005). By contrast, decreased insulin signaling in follicle cells is responsible for the formation of P bodies in nurse cells when nutrients are lacking, and ILP2 overexpression blocks P body formation and leads to a 24% decrease in hatching rates, suggesting a potential role for P bodies in maintaining oocyte quality during starvation (Burn *et al.*, 2015). A developmentally programmed decrease in insulin signaling during later stages of oogenesis initiates glycogen storage (Sieber *et al.*, 2016). Insulin signaling in cap cells controls niche size and adhesion, indirectly affecting GSC maintenance (Hsu and Drummond-Barbosa, 2009). Insulin signaling in adipocytes within the fat body has additional roles in fine-tuning oogenesis (Armstrong and

Drummond-Barbosa, 2018; Bradshaw *et al.*, 2024). The amino acid sensor target of rapamycin (TOR) also acts together with or independently of insulin signaling to control multiple aspects of *Drosophila* oogenesis (LaFever *et al.*, 2010; Sun *et al.*, 2010; Wei *et al.*, 2014; Wei and Lilly, 2014) (Fig. 4). Similarly, knockdown of insulin and TOR pathway components disrupts *T. castaneum* oocyte growth and vitellogenesis and decreases fertility (Parthasarathy and Palli, 2011; Sang *et al.*, 2016). In *Ae. aegypti*, blood feeding causes the release of ILPs, which stimulate DNA synthesis and ecdysteroid hormone production in the ovaries and increase vitellogenin, carbohydrate, and lipid storage by the oocyte (Brown *et al.*, 2008; Vogel *et al.*, 2015; Valzania *et al.*, 2019). Insulin and TOR signaling in response to a blood meal are also important in the mosquito fat body for induction of yolk protein expression (Roy *et al.*, 2007; Roy and Raikhel, 2011). Insulin signaling in *B. germanica* and in the common ladybug *Coccinella septempunctata* (Coleoptera) increases vitellogenin production and oocyte growth (Lenaerts *et al.*, 2019a; Santos *et al.*, 2019). In *Harpegnathos* ants, death of the queen allows workers to become reproductively active in a process that involves increased insulin expression in the brain and vitellogenin and lipid synthesis (Yan *et al.*, 2022). In *R. prolixus*, knockdown of the insulin receptor reduces fat storage and expression of lipid metabolic proteins in the fat body and leads to smaller ovaries and reduced egg production (Silva-Oliveira *et al.*, 2021). Recently generated antibodies against the lepidopteran FOXO—a downstream effector of insulin receptor—and TOR show their expression in the *Heliconius charithonia* (Lepidoptera) fat body (Armstrong and Boggs, 2023), consistent with the role of insulin signaling in the oogenesis of the soybean pod borer *Maruca vitrata* (Lepidoptera) (Al Baki *et al.*, 2019). In the migratory locust *Locusta migratoria* (Orthoptera), one of its two insulin receptors (LmInR2) has a dedicated role in reproduction: it is predominantly expressed in the adult fat body and its knockdown drastically reduces ovarian size due to impairment of endoreplication and vitellogenin synthesis (Yang *et al.*, 2025).

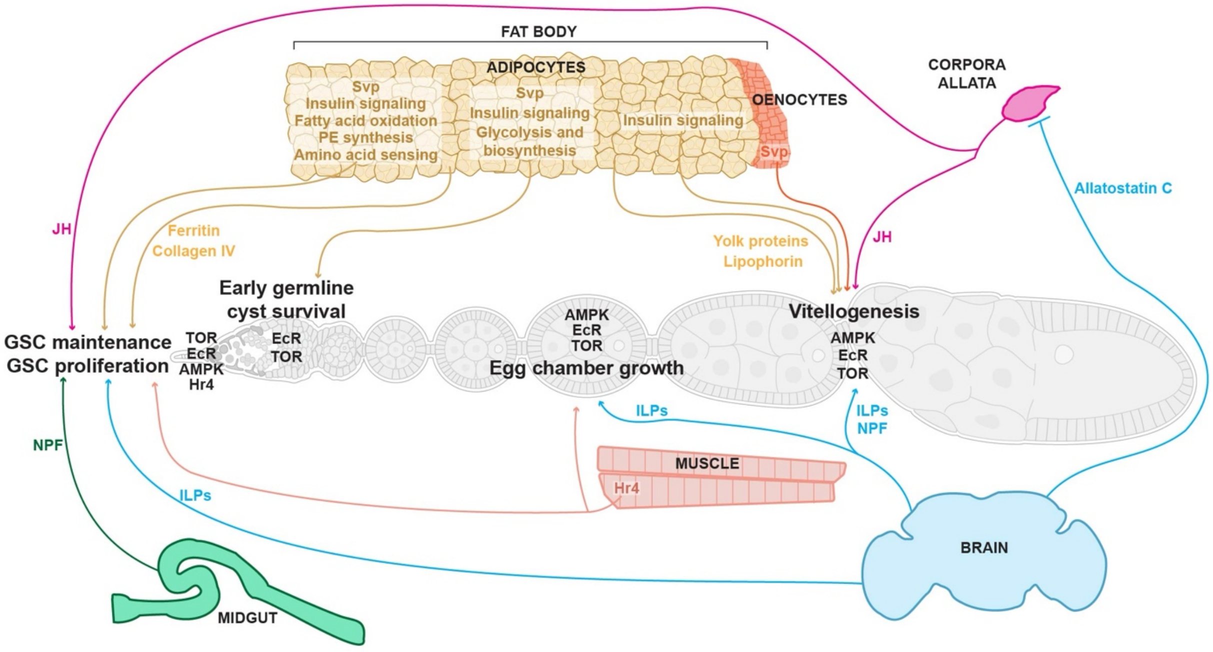

Fig. 4 Diagram of major physiological pathways and interorgan communication controlling *D. melanogaster* oogenesis. Insulin-like peptides (ILPs) produced by neurosecretory cells in the brain on a nutrient-rich diet act on cap cells to promote germline stem cell (GSC) maintenance and on the germline to stimulate the proliferation of GSCs and their early daughters and egg chamber growth and vitellogenesis. The amino acid sensor target of rapamycin (TOR) acts independently of insulin signaling to control GSC maintenance and early germline cyst survival, while working downstream of insulin signaling to promote egg chamber survival and growth (through effects on the germline and follicle cells). The energy sensor AMP kinase (AMPK) is required on a nutrient-poor diet in the germline to inhibit GSC maintenance and promote vitellogenic egg chamber degeneration, and in follicle cells to repress egg chamber growth. Juvenile hormone (JH) produced in the corpora allata controls GSC maintenance and vitellogenesis (by stimulating vitellogenin, or yolk protein, production). Ecdysone produced by vitellogenic follicles acts on its receptor (EcR) to control many processes during oogenesis, including GSC maintenance and proliferation, early germ cell development, nurse cell elimination, vitellogenesis, border cell migration, follicle cell endoreplication, and chorion gene amplification. Brain-derived neuropeptide F (NPF) controls survival of vitellogenic egg chambers according to sensory inputs, while midgut-derived NPF control GSC proliferation in response to mating. Allatostatin C-producing neurons repress JH synthesis and are deactivated upon mating. The nuclear receptor Hormone receptor 4 (Hr4) is required in muscles to promote GSC maintenance and egg chamber growth, while the nuclear receptor Seven up (Svp) is required in oenocytes to control vitellogenesis and in adipocytes to promote GSC maintenance and early cyst survival. In addition to secreting yolk proteins, adipocytes secreted other molecules that modulate oogenesis, including ferritin and collagen IV (required for GSC maintenance) and lipophorin (required for lipid uptake). Adipocytes also influence multiple processes of oogenesis downstream of insulin signaling, amino acid signaling, and metabolic pathways, including fatty acid oxidation, phosphatidylethanolamine (PE) synthesis, glycolysis and biosynthesis.

The Venus kinase receptor is a receptor tyrosine kinase present in many insects (but absent in *D. melanogaster*) that has similar domains to the insulin receptor, induces insulin-like intracellular pathways, but does not bind ILPs (Dissous, 2015). The Venus kinase receptor is expressed in the ovaries of *T. castaneum*, *A. mellifera*, *A. gambiae* and *Ae. aegypti* (Dissous, 2015). The ligand for the Venus kinase receptor appears to vary depending on the insect species. In *Ae. aegypti*, a neuroparsin family member, ovary ecdysteroidogenic hormone (OEH), is the ligand for Venus kinase receptor (Vogel *et al.*, 2015). OEH is released (from the same brain medial neurosecretory cells that release ILPs) in response to blood feeding and stimulates oocytes to take up yolk and the ovary to produce ecdysteroids that induce fat body production of yolk proteins (Dissous, 2015). The amino acid L-arginine was shown *in vitro* to be a potent agonist of the Venus kinase receptor encoded by the mosquito *Anopheles coluzzii* (Diptera) (Gouignard *et al.*, 2019). However, this receptor does not appear to be required for oocyte development or fertility, instead having roles in larval growth and immunity against *Plasmodium* (Gouignard *et al.*, 2019). L-arginine also binds and stimulates the *A. mellifera* Venus kinase receptor *in vitro* (Ahier *et al.*, 2009). In the desert locust *Schistocerca gregaria* (Orthoptera), the Venus kinase receptor is expressed at low levels in the ovaries, its knockdown has no effects on female fertility, and its ligand has not been identified (Lenaerts *et al.*, 2017). The Venus kinase receptor ligands and their potential roles in the oogenesis remain unknown in most of the studied insect species.

AMPK

The AMP-activated protein kinase (AMPK) is an evolutionarily conserved protein present in virtually all eukaryotes that senses cellular energy status to control many metabolic and developmental processes (Sinnett and Brenman, 2016; Cavinato *et al.*, 2021). AMPK has been studied in the context of larval stages and metamorphosis (Rider *et al.*, 2011; Yuan *et al.*, 2020; Zhao *et al.*, 2023; C. Zhang *et al.*, 2025a), but its role in insect oogenesis has not been widely investigated. In *D. melanogaster*, AMPK helps mediate the slowdown in GSC and follicle cell proliferation, as well as the vitellogenesis block that occurs in response to a poor diet (Fig. 4). In addition, AMPK is required in follicle cells to limit the growth of the underlying germline cyst on a poor diet (Laws and Drummond-Barbosa, 2016). In *Ae. atropalpus*, pharmacological activation of AMPK causes delayed follicle development (Telang *et al.*, 2015). Finally, in *T. castaneum*, AMPK activation in response to insecticides alters the expression of oogenesis regulators and has been proposed to mediate a tradeoff between detoxification and reproduction (Jiang *et al.*, 2023).

Juvenile hormone and ecdysteroids

Juvenile hormone

Juvenile hormones (JHs), which are hydrocarbon compounds belonging to the class of sesquiterpenoids, are produced by a pair of endocrine glands called the corpora allata and play crucial roles in insect oogenesis. In many insects, JH synthesis is regulated by neuropeptides, ecdysteroids, diet, insulin and TOR signaling, and mating, and it acts through a nuclear receptor to control gene expression in target tissues (Noriega, 2014; Santos *et al.*, 2019; Knapp *et al.*, 2022). In some cases, JH is also actively degraded under periods of reproductive stress. For example, in the cabbage beetle *Colaphellus bowringi* (Coleoptera) and in the ladybug *C. septempunctata*, JH degradation enzymes are upregulated in response to low JH levels in females destined for reproductive diapause to reinforce the diapause phenotype (Guo *et al.*, 2019; Li *et al.*, 2022). By contrast, JH degradation does not appear necessary for reproductive diapause in *H. axyridis* (Gao *et al.*, 2022).

JH is required for vitellogenesis in nearly all insects. JH increases vitellogenin production in the fat body, supports oocyte growth and maturation, and in some insects controls patency in follicle cells to allow hemolymph to reach the oocyte (Roy *et al.*, 2018; Santos *et al.*, 2019; Wu *et al.*, 2021). The roles of JH have been extensively studied in *L. migratoria* (Roy *et al.*, 2018; Santos *et al.*, 2019; Song and Zhou, 2020). For example, JH induces polyploidy and vitellogenin production in the fat body by regulating the expression of many factors, including DNA replication enzymes, cell cycle regulators, a sugar transporter, and the insulin receptor LmInR2 (Wu *et al.*, 2018, 2020; Zeng *et al.*, 2020, 2022). JH also stimulates the phosphorylation of the vitellogenin receptor, which is required for its binding to vitellogenin on the oocyte surface prior to endocytosis (Jing *et al.*, 2021). In *Ae. aegypti*, JH signaling is required shortly after eclosion in previtellogenic females for follicle cell differentiation in early stages of oogenesis (Raikhel and Lea, 1991) and for the fat body to become competent to produce large amounts of vitellogenins—by stimulating insulin signaling to increase lipid and glycogen reserves (Zhao *et al.*, 2024) and by increasing ribosome biogenesis through the increased expression of ribosomal RNA, several ribosomal proteins, and regulator of ribosome synthesis 1 (Raikhel and Lea, 1990; Wang *et al.*, 2017). JH stimulates insulin signaling to promote vitellogenin expression by the fat body in newly eclosed *T. castaneum* females (Sheng *et al.*, 2011). JH also influences vitellogenin production in other insects, including the cockroach *B. germanica*, the termite *Reticulitermes speratus* (Blattodea), the fruit fly *D. melanogaster*, and a subset of lepidopterans (Santos *et al.*, 2019) (Fig. 4). By contrast, in *B. mori*, *H. cecropia*, and *Spodoptera frugiperda* (Lepidoptera), vitellogenin is synthesized prior to adult eclosion, suggesting that JH does not have a major role in vitellogenesis (Wu *et al.*, 2021).

JH has additional roles in insect female reproduction. In *D. melanogaster*, JH has been reported to regulate cap cell and GSC maintenance (Suyama *et al.*, 2023) and egg length (Luo *et al.*, 2021), while neuronal suppression of JH production in the corpora allata is required for reproductive diapause (Kurogi *et al.*, 2023). A study in the tsetse fly *G. morsitans* suggested that JH levels increase during the dry phase and decrease during lactation and showed that JH stimulates lipid storage and is important for fertility (Baumann *et al.*, 2013). Other studies showed that JH regulates reproductive diapause in many additional insects, including *Chrysoperla nipponensis* (Neuroptera), *Riptortus pedestris* (Hemiptera), *C. bowringi*, *C. septempunctata*, and *Galeruca daurica* (Coleoptera) (Duan *et al.*, 2022; Li *et al.*, 2022; Hafeez *et al.*, 2025; Huang *et al.*, 2025; Tian *et al.*, 2025; Wang *et al.*, 2025).

Ecdysteroids

Ecdysteroids are steroid hormones that regulate oogenesis in multiple insects, and their levels are regulated by diet and insulin signaling in many insects, and also by caste level in social insects (Luna-Lucena *et al.*, 2018; Roy *et al.*, 2018; Khalid *et al.*, 2021). In the parasitoid wasp *Eupelmus vuilleti* (Hymenoptera), the presence of its plant host induces ovarian production of ecdysteroids (Bodin *et al.*, 2007). In *D. melanogaster*, the main ecdysteroid—20-hydroxyecdysone (hereafter ecdysone)—is produced by vitellogenic follicles and has many direct and indirect roles during oogenesis (Roy *et al.*, 2018; Drummond-Barbosa, 2019) (Fig. 4). Ecdysone controls GSC maintenance and proliferation, early germ cell development, nurse cell elimination, lipid uptake by oocyte and vitellogenesis, border cell migration, follicle cell endoreplication, chorion gene amplification, and eggshell production in the ovary (Buszczak *et al.*, 1999; Hackney *et al.*, 2007; Sun *et al.*, 2008; Bernardi *et al.*, 2009; Jang *et al.*, 2009; Ables and Drummond-Barbosa, 2010; König *et al.*, 2011; Morris and Spradling, 2012; Ables *et al.*, 2016; Ghosh *et al.*, 2025). In addition, ecdysone increases triglyceride and glycogen storage in the fat body and stimulates female feeding (Sieber and Spradling, 2015).

In the mosquito *Ae. aegypti*, a blood meal triggers the release of brain neurohormones that stimulate ecdysone production, which in turn promotes vitellogenin synthesis in the fat body (Sappington and Raikhel, 1998; Roy *et al.*, 2018). The ecdysone target E93 is upregulated by ecdysone and downregulated by JH, and its regulation by these two hormones controls reproductive cycle switches (Wang *et al.*, 2021), while E75 senses heme to activate ecdysone-induced gene expression, including vitellogenin, in the fat body (Cruz *et al.*, 2012). In *D. melanogaster* and *Ae. aegypti*, ecdysone can regulate JH production (Areiza *et al.*, 2014; Leyria, 2024). Interestingly, ecdysteroids are transferred from males during mating to promote oocyte development via interactions with the mating-induced stimulator of oogenesis protein in *A. gambiae* (Baldini *et al.*, 2013). The role of ecdysone in supporting *B. mori* vitellogenesis and transition into choriogenesis appears similar to that in *D. melanogaster* (Swevers and Latrou, 2003; Zhu *et al.*, 2021), and ecdysteroids can also alter the levels of some maternal mRNAs in the oocyte (Zhang *et al.*, 2021). In *T. castaneum*, ecdysone (but not JH) regulates primary oocyte maturation and growth and migration of follicle cells (Parthasarathy *et al.*, 2010). Knockdown of the ecdysone responsive gene E93 in newly emerged adults decreases vitellogenin synthesis and lipid droplet number and size in the fat body and prevents oocytes from developing past previtellogenic stages 1 or 2 (Eid *et al.*, 2020). Similarly, ecdysone controls vitellogenesis in *C. bowringi* (Wang *et al.*, 2023). Ecdysone is critical for *R. prolixus* oogenesis (Benrabaa *et al.*, 2023), and ecdysteroids are also important in insects with panoistic ovaries. For example, in *S. gregaria*, ecdysteroids control oocyte development and choriogenesis (Lenaerts *et al.*, 2019b; Schellens *et al.*, 2022), while ecdysone has been reported to affect multiple steps of oogenesis in *B. germanica* (Rumbo *et al.*, 2023).

Other physiological factors

Brain neuropeptides and biogenic amines

Neuropeptides and monoamines produced in the brain help coordinate insect oogenesis (Fig. 4). As described above, ILPs are the best studied neuropeptides with roles in insect oogenesis and the neuroparsin OEH helps induce ovarian ecdysteroid production in response to nutrients in *Ae. aegypti* (Vogel *et al.*, 2015; Valzania *et al.*, 2019). Many other neuropeptides are required for insect oogenesis (Van Wielendaele *et al.*, 2013; Lenaerts *et al.*, 2019a; Knapp *et al.*, 2022). For example, in *T. castaneum* and in *B. tabaci*, knockdown of neuropeptides bursicon and partner of bursicon decreases JH and vitellogenin production (Li *et al.*, 2021; Yu *et al.*, 2023). Neuropeptide F (NPF) has been implicated in supporting oogenesis in multiple species (Lenaerts *et al.*, 2019a). For example, in *D. melanogaster*, gut-derived NPF has been proposed to regulate GSC proliferation in response to mating (Ameku *et al.*, 2018), while brain-derived NPF controls the survival of vitellogenic egg chambers downstream of sensory inputs (Sadanandappa *et al.*, 2021). Allatostatin C-producing neurons repress JH synthesis and are deactivated through a mechanism involving sex peptide upon mating (Zhang *et al.*, 2022). Octopamine is a monoamine that is made in octopaminergic neurons that innervate the female reproductive tract and regulates multiple aspects of female insect reproduction (White *et al.*, 2021).

Adipocytes, oenocytes, and muscles

Multiple organs contribute to the regulation of insect oogenesis. For example, we discussed the importance of JH from the corpora allata, ILPs and other neuropeptides from the brain, and vitellogenin from the fat body. Studies in *D. melanogaster* suggest that there is much more to be discovered regarding how various organs contribute to the fine modulation of different processes in insect oogenesis (Fig. 4). For example, adipocyte-specific disruption of various metabolic pathways, including amino acid sensing, fatty acid oxidation, phosphatidylethanolamine synthesis, or iron transport, can lead to GSC loss or death of early germline cysts (Armstrong *et al.*, 2014; Matsuoka *et al.*, 2017). Similarly, various adipocyte-derived signaling proteins (i.e., adipokines) influence early and late germline survival (Simmons *et al.*, 2025). Adipocyte-derived collagen IV is transported to the GSC niche, where it promotes E-cadherin-mediated adhesion to GSCs and thereby GSC maintenance (Weaver and Drummond-Barbosa, 2018). The nuclear receptor Seven up—which regulates immunity and xenobiotic response genes in the fat body (Weaver and Drummond-Barbosa, 2020)—is required in adipocytes for GSC maintenance and early germline cyst survival and in oenocytes for vitellogenesis (Weaver and Drummond-Barbosa, 2019). The nuclear receptor Hormone receptor 4 is required in muscles for GSC maintenance and egg chamber growth (Weaver and Drummond-Barbosa, 2021). In some migratory insects, flight performance is thought to negatively correlate with female fecundity, a concept termed oogenesis-flight syndrome (Wheeler, 1996; Isaacs and Byrne, 1998; Tigreros and Davidowitz, 2019; Ge *et al.*, 2021), although this idea has been challenged in the past (Sappington and Showers, 1992). Regardless, much remains unknown about the potential mechanisms involved.

Immune system

Oogenesis and immune responses also interact in insects. Insects that mate more frequently have lowered immunity owing to increased JH production and allocation of energy to reproduction (Nunes *et al.*, 2021). *D. melanogaster* females without germ cells do not have reduced immunity after mating (Nunes *et al.*, 2021). Depletion of metals, such as zinc, iron, and copper, which are common responses against pathogens, can also reduce insect female fecundity (Cardoso-Jaime *et al.*, 2022). Conversely, eicosanoids play an important role in insect cellular immunity, but also stimulate egg laying, yolk protein uptake, and proper nuclear shape in ovary development of some insects (Stanley, 2006; Talbot *et al.*, 2023). In multiple insects, vitellogenins contribute to vertical transmission of symbionts or defense against nematodes, fungi, bacteria, or venoms (Wu *et al.*, 2021; Kodrik *et al.*, 2023).

Conclusion

Insects represent one of the most evolutionarily successful classes of animals, in large part owing to their remarkable reproductive prowess. Insect females have a pair of ovaries that vary widely in terms of ovariole numbers, and they have evolved three basic types of ovariole structures. Many studies have investigated the major processes in polytrophic meroistic ovarioles, such as those in the *D. melanogaster* model organism, but relatively less is known regarding panoistic and telotrophic meroistic ovarioles. Adult GSCs are generally absent from telotrophic meroistic ovarioles, while in panoistic and polytrophic meroistic ovarioles the presence of GSCs depends on the species. Whether insects produce eggs continuously or in bursts depends on their type of diet but, in all insects, oogenesis is responsive to a variety of environmental and other stimuli to maximize reproduction under ideal conditions. This high degree of regulation of oogenesis presumably results from strong evolutionary pressure to avoid wasting resources under adverse conditions; for example, if females continued to lay large numbers of eggs when nutrients are scarce, they would waste precious resources and jeopardize their own survival (and future chances to reproduce) as well as the odds of their own progeny to develop and thrive to perpetuate the species. The complex physiological network that ensures the fine regulation of oogenesis shares many common themes among diverse insects. For example, the cost-intensive process of vitellogenesis is widely regulated by JH, ecdysteroids, or both in virtually all insects, and insulin and TOR signaling also appear to have conserved roles—although there are many differences and unknowns in the detailed mechanisms of action. There are also apparently uncommon strategies in the regulation of oogenesis of some insects, including transfer of ecdysteroids or nutrients through mating or specific symbiotic interactions. The best studied external oogenesis stimulus is diet, while the effects of other factors such as temperature, humidity, pheromones, immune responses, circadian rhythm, physical activity, social interactions, or microorganisms are much less well understood. Very little is known about the regulation of adult GSCs or equivalent developmental germ cell precursors in any insect aside from *D. melanogaster*. In addition, much remains unknown about the regulation of follicle formation or pre-vitellogenic development in most insects other than *D. melanogaster*, or about the ways in which adipocytes, oenocytes, muscles, nervous system, midgut, and other organs contribute to the fine tuning of oogenesis in response to various factors. Further developments in genomics, cell biological, and genetic tools (including for tissue-specific manipulation) in a wider range of insects will greatly contribute to answering many of these open questions. What is overwhelmingly clear is that the current stage of knowledge in the field of insect oogenesis represents the very tip of the iceberg—a treasure trove of fascinating biology with wide relevance to basic science, ecology, food security, and human health (Table 1).

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