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苹果蠹蛾卵成熟过程及卵巢发育分级研究

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摘 要:【目的】研究苹果蠹蛾卵的成熟过程和卵巢发育特征及其分级。**【方法】**采用常规解剖和石蜡切片方法,对苹果蠹蛾卵粒在卵巢管中的成熟过程进行观察,并对其卵巢发育及分级进行划分。**【结果】**苹果蠹蛾卵成熟过程根据卵粒大小、滋养细胞和滤泡细胞的形态变化以及卵黄沉积情况,分为卵黄发生前期、早期卵黄发生期、中期卵黄发生期、后期卵黄发生期和成熟期5个时期。卵巢发育根据有无卵室、卵黄沉积情况和卵巢形状划分为5个级别,即:发育初期(Ⅰ级)、卵黄沉积期(Ⅱ级)、成熟待产期(Ⅲ级)、卵盛期(Ⅳ级)和产卵末期(Ⅴ级)。**【结论】**明确了卵粒在成熟过程中的形态变化和苹果蠹蛾卵巢发育的分级特征,为准确进行该虫的预测预报和综合防治提供了科学依据。

关键词: 苹果蠹蛾;卵巢发育;卵成熟过程;组织学

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Study on the process of egg maturation and classification of ovary development in codling moths (*Cydia pomonella* L.)

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Abstratc:【Objective】The codling moth is a kind of quarantine pests of fruit trees in both China and the world because of its severe damage and strong fecundity. The egg-laying amount in nature is much higher than that in laboratory level, reaching more than 300 eggs. Thus, it is of great significance to study the process of egg maturation and ovary development with the codling moths. The aim of this study is to observe the process of egg maturation in Varian tubules and the developmental characteristics of ovaries in different stages after the emergence of female adults, which will provide a basis for the integrated management of the codling moths.【Methods】The larvae of codling moth were originally collected from an abandoned apple orchard, Wuwei city nearby, Gansu province and maintained under standard laboratory conditions at (25±1)℃ with a relative humidity of 75%±5%, and a 16/8 light/dark cycle. The larvae of codling moths were reared up to the adult stage in spawning boxes by providing 10% honey water. When the process of eggs maturation was studied, the female adults emerging after 24-48 h were dissected in the chilled insect ringer solution and observed under a stereoscopic binocular microscope for anatomical observations. The ovaries were fixed in Bouin's fixative for 12 h and washed in water and then dehydrated gradually with the ethyl alcohol. After dehydration, tissues were cleared in n-butyl alcohol, infiltrated and embedded in paraffin wax at 60 ℃. Tissues were sectioned at 5 μm after the clotting of the tissue block. Sections were stained with Haematoxylene-Eosin. The slices were observed and photographed under a binocular EX20 fluorescence microscope. In order to examine the developmental process of ovaries, a female adult and a male adult on the same day of age were collected

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into a disposable plastic cup (6-8 cm in diameter). The plastic cups were sealed by using a fresh-keeping bag with the absorbent cotton with 10% honey water. The fixed (30 min) insect body was dissected day by day in a Petri dish with Ring's physiological saline under the Motic K series anatomy microscope. The morphological structures of the ovaries were observed under the Zeiss Stereo Discovery V12 stereoscopic microscope, photographed with a AxioCamMRc 5 and the pictures were processed with Adobe Photoshop.【Results】The process of egg maturation of codling moths was divided into five stages according to the size of the eggs, the morphological changes of the follicular and trophoblast cells, and the yolk deposition, which were named the previtellogenesis stage, the early stage of vitellogenesis, the middle stage of vitellogenesis, the late stage of vitellogenesis and maturation stage, respectively. A few cells on the top and a large number of cells on the lower took place in the egg at the previtellogenesis. Eggs were nearly round at the early stage of vitellogenesis and surrounded by 1-2 layers of cells except for follicular cells that were arranged loosely. There were different sizes of droplets in whole eggs after they grew into the oval shape at the middle stage of vitellogenesis. The shapes of follicular cells in epithelial tissue were spherical to oval. The trophoblastic cells gradually decreased. In the late stage of yolk occurrence, the egg volume became larger, and the yolk drops dispersed in the whole cytoplasm at the late stage of vitellogenesis. At this stage, the follicle membrane was composed of dense squamous epithelial cells, and the trophoblastic cells almost disappeared. The maturation stage was the last period of the development of the egg. Eggshell formed when the egg increased to a certain size but there was no trophoblast at this stage. The ovarian development of codling moths was divided into five phases according to the shapes of ovary, yolk deposition and appearance or disappearance of an egg chamber, which were named the initial phase (Stage Ⅰ), yolk deposition phase (Stage Ⅱ), egg maturation phase (Stage Ⅲ), peak phase of oviposition (Stage Ⅳ) and terminal phase of oviposition (Stage Ⅴ), respectively. Stage Ⅰ: The tube of the ovary was very small with no egg chamber forming within the growth area of the ovarian tube and was transparent. Fat body was spherical and milky white. There were no eggs in ovarian tube handle, lateral fallopian tube and middle fallopian tube. Stage Ⅱ: The ovarian tube thickened and grew. The yolk sediments were filled with the egg chamber, and there was an obvious overflowing margin between the egg chambers. The adipocytes became oblong with milky white color. Stage Ⅲ: The ovarian tube became thicker and the boundaries between the egg chambers were not obvious. The fat body cells were long filamentous and the eggs arranged closely in the lateral fallopian and middle fallopian tubes. Stage Ⅳ: The boundary between the egg chambers disappeared. The fat body was significantly reduced and almost depleted. The eggs in the lateral fallopian tube and the middle oviduct were high and easy to fall off. Stage Ⅴ: There was a boundary between the egg chambers. The remaining mature eggs containing about 3-4 grains existed in the growing area of the ovarian tube. The ovarian tube base was orange yellow and the fat body was depleted.【Conclusion】In this study, we observed the morphological change of the egg and ovarian development stages of the codling moth, which could provide a scientific reference for forecasting and integrated management on this pest.

Key words: *Cydia pomonella*; Ovarian development; Egg development; Histology

苹果蠹蛾（*Cydia pomonella* L.），属鳞翅目（Lepidoptera）卷蛾科（Tortricidae），是世界性检疫害虫，也是我国主要的苹果害虫检疫对象。首次发现于新疆库尔勒[1]。该虫危害严重主要与其取食范围广、个体繁殖能力强等生物学特性密切相关。目前，对苹果蠹蛾的研究主要集中在生物学、生态学习性[2-3]、人工饲料及配比[4]、苹果蠹蛾颗粒体病毒[5]、抗药性[6]和抗性基因的克隆[7]等方面。对其卵巢发育状况和卵粒成熟过程的研究未见报道。

昆虫种群数量的变动与环境条件、昆虫个体的

行为和繁殖特点直接相关，而这些复杂因素的综合作用在昆虫的生殖系统中有不同程度的反映[8]。昆虫的卵巢通常成对，位于消化道的背面，各由一组数量不等的卵巢管组成，具有贮存和增殖生殖细胞的功能。

通过对昆虫生殖系统发育过程的研究可获得应用于昆虫预测预报的指标[9-11]。如刘绍友等[12]将小地老虎的卵巢发育进度分为5级；为了加强对二化螟种群的发生期和发生量的预测，对其发育级别进行了划分[8]。张韵梅等[13]、钱仁贵[14]、王宪辉等[15]和王晓芳等[16]分别对棉铃虫、玉米螟、甜菜夜蛾和迁粉蝶进行了研究。Gaikwad等[17]将玉带凤蝶的卵成熟过程分为5个阶段。由此看出，昆虫卵巢和卵子发育过程的研究对害虫种群发生期和发生量的预测预报具有重要的实践意义[18-19]。

因此，笔者通过解剖和组织切片研究苹果蠹蛾卵粒在成熟过程中的形态变化和卵巢发育进度，为生产实践中苹果蠹蛾种群发生期和发生量的预测预报和综合防治提供参考，同时为进一步研究其胚胎发育奠定基础。

1 材料和方法

1.1 供试虫源

从甘肃省武威市废弃苹果园内采集蛀果，幼虫用幼果饲养，成虫供以10% 蜂蜜水，饲养条件为温度(25±1)℃，相对湿度(75±5)%，光周期L(光照)∶D(黑暗)= 16 h∶8 h。

1.2 供试药剂和仪器

1.2.1 试剂 Bouin's液、Ring's生理盐水、石蜡(上海华申康复器材有限公司)、10%(φ，后同)甲醛、50%乙醇、70%乙醇、80%乙醇、95%乙醇、无水乙醇、正丁醇、醇蜡(正丁醇∶石蜡=1∶1)、蜡Ⅰ、蜡Ⅱ、二甲苯、苯酒(二甲苯∶酒精=1∶1)、盐酸分化液、蒸馏水、自来水、Weigert氯化铁苏木精、伊红、中性树胶。

1.2.2 仪器 Stereo Discovery V12型体视显微镜(北京博瑞斯科技有限公司)、Motic K series型解剖镜、手术刀、解剖针、尖头镊子、小烧杯、载玻片、盖玻片、滴瓶、吸管、小培养皿(直径3 cm)、无菌水、Leica RM2253半自动轮转式切片机(北京长恒荣创科技有限公司)、KD-P摊片机(浙江省金华市科迪仪器设备有限公司)、KD-H烘片机(浙江省金华市科迪仪器设备有限公司)、KD-BM生物组织包埋机(浙江省金华市科迪仪器设备有限公司)、Leica光学显微镜、双目EX20荧光显微镜、染色架、秒表、电热恒温培养箱。

1.3 方法

1.3.1 卵巢发育过程观察 收集同一日龄羽化的成虫置于一次性塑料杯(直径6~8 cm)内配对饲养，用保鲜袋封住杯口。保鲜袋中夹带浸有10%蜂蜜水的脱脂棉作为成虫补充营养源。逐日解剖成虫。将固定(30 min)后的虫体放入滴有Ring's生理盐水的小培养皿中，在Motic K series解剖镜下进行解剖，在Zeiss Stereo Discovery V12体视显微镜下进一步观察解剖，用AxioCamMRc 5拍照，Adobe Photoshop CS6进行图片处理。

1.3.2 卵巢管形态及卵粒成熟过程观察 解剖羽化24~48 h的苹果蠹蛾成虫，取其卵巢，即刻放入Bouin's固定液中，固定12 h。流水冲洗4 h之后，经酒精梯度脱水、正丁醇透明、浸蜡、包埋、5 μm连续切片，展片，苏木精-伊红染色、中性树胶封片等过程。切片在双目EX20荧光显微镜下观察并拍照。

2 结果与分析

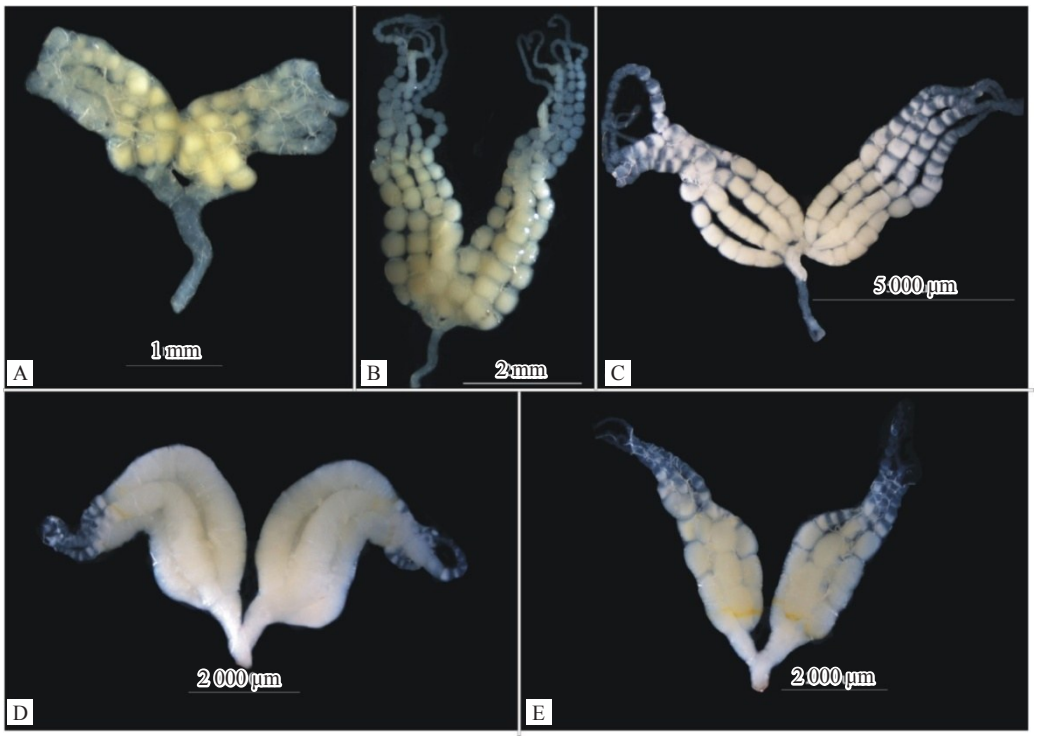
2.1 卵巢发育分级

如图1所示，根据0~8日龄不同卵巢管的发育特征，将其分为5个级别：

Ⅰ级(0~0.5日龄)发育初期(图1-A)：卵巢管细小，每侧卵巢管通过隔膜、脂肪体及微气管紧紧合并在一起，不易分散。卵巢管端部的生长区尚未形成卵室，呈透明状，近基部的生殖区发现卵黄沉积物。脂肪体呈饱满的圆球形，乳白色，充满腹腔并包围两侧卵巢。卵巢管柄细长，侧输卵管及中输卵管较粗；三者均为透明状，里面没有卵细胞存在。

Ⅱ级(0.5~1日龄)卵黄沉积期(图1-B)：卵巢管增粗变长，每侧卵巢管通过隔膜、脂肪体及微气管螺旋缠绕在一起，较Ⅰ级卵巢贴的更为紧密。卵黄沉积物充满卵室空间，卵室之间有明显的溢缩界限。腹腔内脂肪体仍较满，脂肪细胞变长圆形，乳白色。

Ⅲ级(1~2日龄)成熟待产期(图1-C)：卵巢管较Ⅱ级粗。卵室之间界限较清晰但没有Ⅱ级中的明显，基部的卵室可见乳白色膨大的未成熟卵。腹腔内脂肪体较Ⅱ级卵巢少，脂肪体细胞呈长形丝状。卵巢管柄不明显，侧输卵管和中输卵管中存有卵粒，且排列紧密。



A. Ⅰ级，发育初期; B. Ⅱ级，卵黄沉积期; C. Ⅲ级，成熟待产期; D. Ⅳ级，产卵盛期; E. Ⅴ级，产卵末期。

A. Stage Ⅰ, the initial stage; B. Stage Ⅱ, yolk deposition phase; C. Stage Ⅲ, egg maturation phase; D. Stage Ⅳ, peak phase of oviposition; E. Stage Ⅴ, terminal phase of oviposition.

图 1　卵巢管发育分级

Fig. 1 The grade of ovary

Ⅳ级(2~8日龄)产卵盛期(图1-D)：每侧4支卵巢管变得更粗，且为乳白色。卵室之间界限消失。卵巢管柄、侧输卵管及中输卵管膨大，卵室中的卵细胞充满卵巢管柄、侧输卵管和中输卵管。腹腔内脂肪体明显减少，几乎耗尽，白色丝状气管缠绕在卵巢周围。侧输卵管及中输卵管中的卵粒成熟度高，易脱落。

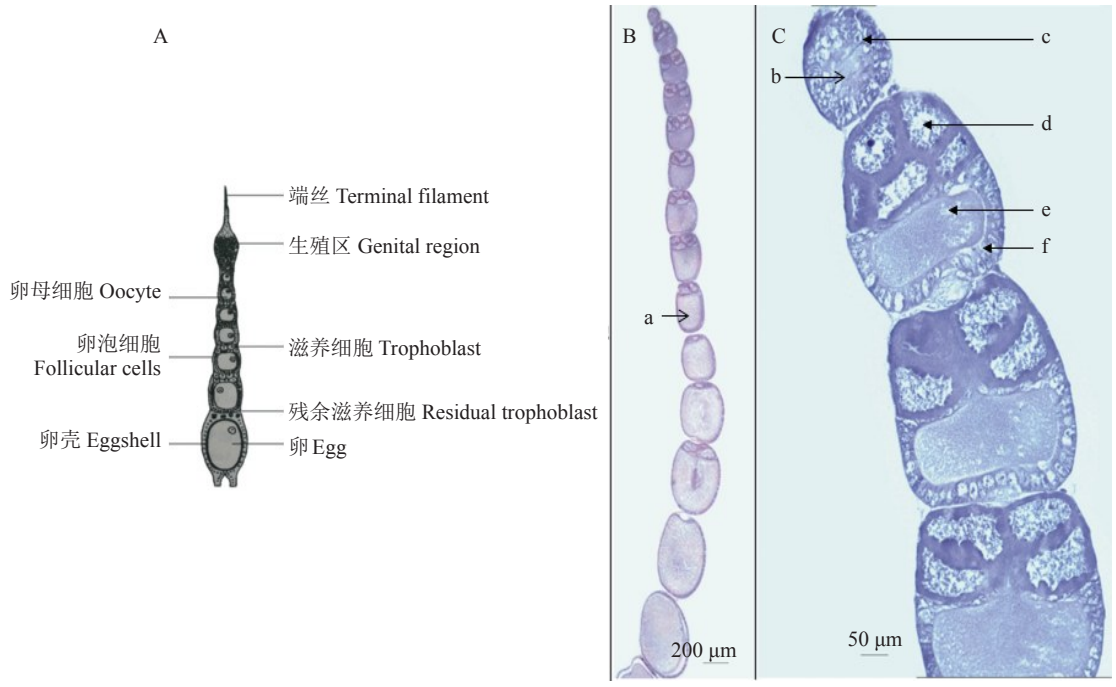
Ⅴ级(8日龄及以上)产卵末期(图1-E)：两侧卵巢管变短，卵室间又出现界限。卵巢管端部生长区卵巢管中残存的成熟卵不多，每条卵巢管大约3~4粒，卵巢管基部靠近卵巢管柄处变为橙黄色进而变为橘黄色。腹腔内脂肪体消耗殆尽，仅存极少数丝状气管围绕在卵巢周围。

2.2　卵巢管形态结构

苹果蠹蛾卵巢管属于多滋式卵巢管(图2)，分为端丝(terminal filament)、卵巢管本部(egg-tube)和卵巢管柄(pedicel)。卵巢管本部前端的围鞘延伸成端丝，并将卵巢悬附于脂肪体、体壁或背膈上。卵子发生和发育在卵巢管本部进行。成熟卵粒通过卵巢管柄进入侧输卵管，卵巢管柄是1条薄壁短管。整个卵巢管外围包被一层管壁膜。当卵粒成熟或落入侧输卵管后，才可见清晰的管壁膜。生殖区分布着卵原细胞、原始卵母细胞和卵母细胞，卵母细胞比较分散，处在生殖区下端。生长区包含卵细胞，滤泡细胞和滋养细胞，卵细胞外层由滤泡细胞组成的细胞层包被，卵细胞通过滋养细胞获取营养。

2.3　卵成熟过程

由图3可以看出，苹果蠹蛾卵的成熟过程分为卵黄发生前期、早期卵黄发生期、中期卵黄发生期、后期卵黄发生期和成熟期5个阶段。卵上方排列有滋养细胞，两侧及下方紧密排列有滤泡上皮细胞。卵黄发生前期的卵，在顶部可见少量细胞，下部有大量的细胞充斥在卵内(图3-A)。早期卵黄期的卵子近圆形(图3-B~C)。除滤泡细胞外还有1~2层细胞围绕着卵，滤泡细胞排列松散。处在卵黄发生中期的卵子生长速度很快，生长成卵圆形后在其整个卵中松散地分散有不同大小的液滴状物质。上皮组织的滤泡细胞排列呈球形至椭圆形。滋养细胞逐渐减少(图3-D~E)。处在卵黄发生后期的卵体积变得更大，卵黄滴分散在整个细胞质中；在此阶段，滤泡包膜由致密的鳞状上皮细胞组成，滋养细胞几乎消失

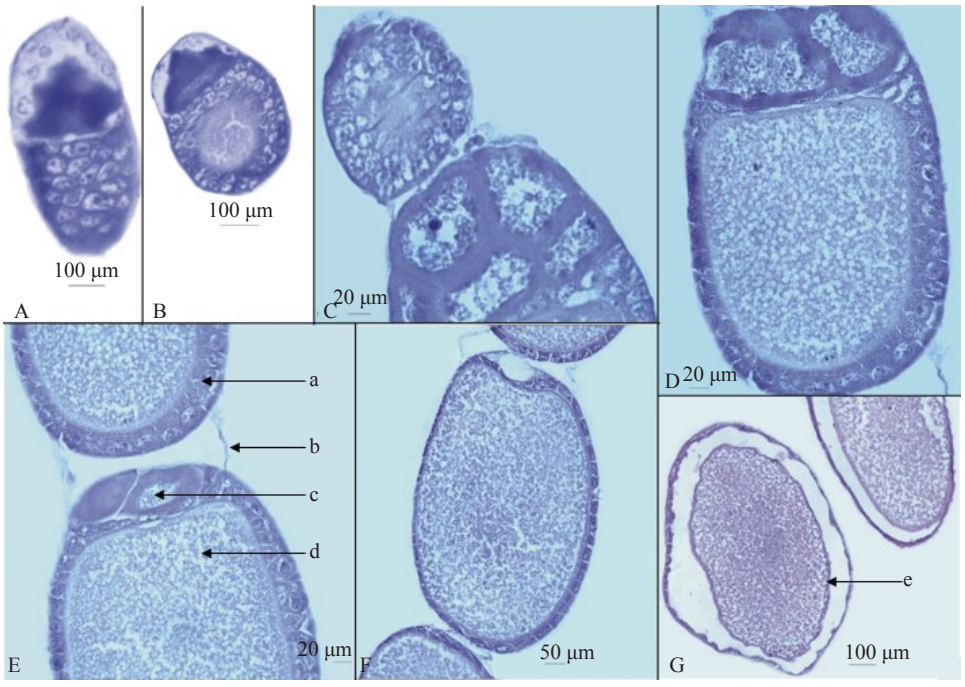


A.昆虫卵巢管的结构与类型(多滋式)仿 Weber，1936；B.苹果蠹蛾卵巢管形态；C.卵巢管放大图。a.卵粒；b.早期卵黄发生期的卵子；c.细胞核；d.滋养细胞；e.中期卵黄发生的卵子；f.滤泡细胞。

A. Structure and type of insect ovary tube (Polytrophic type) (after Weber，1936); B. Form of ovary tube of codling moth; C. Enlarged view of ovarian tube. a. Egg granule; b. Egg at the early stage of yolk occurrence; c. Nucleus; d. Trophoblast; e. Egg at the mid stage of yolk occurrence; f. Follicular cells.

图 2 卵巢管形态

Fig. 2 Morphology of ovary tube



A. 卵黄发生前期的卵；B、C. 早期卵黄发生期的卵；D~F.中期到后期卵黄发生的卵子纵切；G.成熟的卵。a.滤泡细胞；b. 卵巢管膜；c.减少的滋养细胞；d.逐渐增大的卵子和增多的卵黄颗粒；e.卵壳。

A. Egg during the early stage of yolk occurrence; B，C. Egg at the early stage of yolk occurrence; D-F. Longitudinal sections of egg at the mid and late yolk occurrence; G. Mature egg. a. Follicular cells; b. Ovarian duct membrane; c. Reducing trophocytes; d. Increasing egg and yolk granules; e. Eggshell.

图 3 卵成熟过程

Fig. 3 Maturation process of the eggs

殆尽（图3-F）。成熟期是卵发育的最后一个时期。卵增大到一定大小时，形成卵壳。卵壳与滤泡细胞分离。此时已无滋养细胞（图3-G）。

3　讨　论

根据解剖结构、羽化天数和体内其他特征，昆虫的卵巢发育一般分为5~6个级别[20-22]。笔者将苹果蠹蛾的卵巢发育分为5级，但研究过程中发现苹果蠹蛾部分雌虫两侧卵巢或同侧不同卵巢管间发育进度不同步，这可能是卵巢管之间存在生长竞争或营养缺乏，导致一些卵巢管发育不良[23]。产卵末期，卵巢管基部靠近卵巢管柄处变为橙黄色进而变为橘黄色。这可能是卵黄沉淀物。此外，苹果蠹蛾卵巢在2日龄已成熟；3~8日龄为雌蛾产卵盛期；8日龄后卵巢管逐渐衰退，进入产卵末期，补充营养似乎并非卵巢发育的必要条件。这与微红梢斑螟的特征相似[24]。

昆虫卵巢管根据滋养细胞的有无和排列方式，分为无滋式、端滋式和多滋式[25-26]。苹果蠹蛾卵巢由8根多滋式卵巢小管组成，每个卵巢小管分为端丝、卵巢管本部和卵巢管柄。卵巢管中，1个卵细胞和多个滋养细胞被滤泡细胞所包被[27]。而苹果蠹蛾卵的成熟过程分为5个时期，与大多鳞翅目昆虫一致[14]。卵巢管吸收营养物质，使卵在一定时期内达到成熟，卵受精后产出体外[28]。苹果蠹蛾卵发育成熟时与卵巢管柄逐渐分离，滤泡细胞与卵细胞之间出现间隙，靠近卵巢管柄处的滤泡细胞减少甚至消失，这可能与卵壳形成有关。Dobens等[29]、Ma等[30]和刘志伟等[31]对果蝇、蝎蛉和孟氏隐唇瓢虫的研究结果中也存在相似的情况。

关于滤泡细胞的凋亡机制，如Ma等[30]认为刘氏蝎蛉的滤泡细胞参与形成不同区域的卵壳；张天澍等[32]通过研究龟纹瓢虫的卵子发生认为滤泡细胞在卵黄膜和卵壳的形成中均起到关键作用。甚至有报道滤泡细胞的退化受到蜕皮激素的调控[33]。但苹果蠹蛾滤泡细胞的退化机制还不清楚，需进一步研究。

另外，本文明确了苹果蠹蛾卵巢管的形态结构、卵巢发育过程及卵成熟过程。其卵子发生将是下一步研究的重点，从而为害虫的预测预报和防治提供更有利的参考和依据。

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