



斑衣蜡蝉雌性生殖系统超微结构

刘佳宁, 秦道正*

(西北农林科技大学植物保护学院, 陕西杨凌 712100)

摘要:【目的】明确斑衣蜡蝉 *Lycorma delicatula* 雌成虫生殖系统整体形态及超微结构特征, 为蜡蝉总科昆虫分类及系统发育探讨提供更多形态学证据。【方法】采用光学显微镜与透射电子显微镜, 观察斑衣蜡蝉雌成虫生殖系统整体形态和各主要器官的超微结构。【结果】斑衣蜡蝉雌成虫生殖系统主要包括1对卵巢、1个中输卵管、1个交配囊、1个交配囊管、1个前阴道、1个后阴道、1个受精囊、1个受精管和2根受精囊附腺。卵巢为端滋式, 由14根卵巢小管组成, 卵室由固有膜、滤泡细胞和卵细胞组成, 卵巢小管中的滋养细胞清晰可见; 中输卵管位于前阴道基部, 由中输卵管腔、上皮细胞、肌肉鞘和基膜组成; 交配囊膨大呈圆球状, 囊壁由上皮细胞、肌肉层和基膜组成; 交配囊管呈圆柱状, 连接交配囊和后阴道, 由肌肉鞘、上皮细胞层和管腔组成; 前、后阴道超微结构相似, 主要由肌肉鞘、基膜、上皮细胞和管腔组成, 但后阴道上皮细胞细胞核周围存在分泌颗粒, 且管腔内有大量微绒毛, 而前阴道壁内包含有大量囊泡结构; 受精管从中输卵管末端延伸至受精囊, 由基膜、厚层肌肉鞘和管腔组成; 受精囊为受精管近末端略膨大的囊状结构, 由肌肉鞘、基膜、上皮细胞和囊腔构成; 雌性受精囊附腺着生于受精囊末端, 为均匀的螺旋管状, 主要由肌肉层、上皮细胞层和附腺中心管腔组成。【结论】斑衣蜡蝉雌性生殖系统与已报道的蜡蝉总科其他类群的雌性生殖系统结构相似, 但卵巢小管数目有差异; 蝉亚目中不同总科雌成虫雌性附腺与受精囊附腺的形态特征存在明显区别; 斑衣蜡蝉雌性生殖系统超微结构与叶蝉总科和沫蝉总科昆虫也存在部分差异。这些差异是否可以作为头喙亚目高级阶元的划分依据仍有待于进一步研究。

关键词: 蜡蝉科; 斑衣蜡蝉; 雌性生殖系统; 形态; 超微结构; 透射电子显微镜

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Ultrastructure of the female reproductive system of *Lycorma delicatula* (Hemiptera: Fulgoridae)

LIU Jia-Ning, QIN Dao-Zheng* (College of Plant Protection, Northwest A&F University, Yangling, Shaanxi 712100, China)

Abstract: 【Aim】 This study aims to clarify the whole morphology and ultrastructure characteristics of the female reproductive system of the spotted lanternfly, *Lycorma delicatula*, so as to provide more morphological evidence for the taxonomy and phylogenetic analysis of the superfamily Fulgoroidea.

【Methods】 The general morphology and ultrastructure of the reproductive system of female adult of *L. delicatula* were observed by light microscope and transmission electron microscope. 【Results】 The reproductive system of female adult of *L. delicatula* mainly includes one pair of ovaries, one common oviduct, one bursa copulatrix, one bursa copulatrix duct, one anterior vagina, one posterior vagina, one spermatheca, one ductus receptaculi and two spermathecal accessory glands. The ovary is telotrophic and consists of 14 ovarian tubules, the egg chamber is composed of tunica propria, follicular cells and

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作者简介: 刘佳宁, 女, 1995年4月生, 陕西汉中, 硕士研究生, 研究方向为昆虫系统学与生物多样性, E-mail: liujianing2121@126.com

* 通讯作者 Corresponding author, E-mail: qindaozh@nwsuaf.edu.cn

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oocytes, and trophoblasts in ovarioles are clearly visible. The common oviduct is located at the ventral part of the anterior vagina, and comprised of lumen, epithelial cells, muscle sheath and basement membrane. The bursa copulatrix is spherical, and the wall is composed of epithelial cells, muscle layer and basement membrane. The bursa copulatrix duct is cylindrical, connecting with bursa copulatrix and posterior vagina, and comprised of muscle sheath, epithelial cell and lumen. The ultrastructure of the anterior and posterior vagina is similar, mainly composed of muscle sheath, basement membrane, epithelial cells and lumen, but there are secretory granules around the nucleus of the posterior vagina epithelial cells and lots of microvilli in the lumen, while there are lots of vesicles in the anterior vagina wall. The ductus receptaculi extends from the end of common oviduct to spermatheca and consists of basement membrane, thick muscular sheath and lumen. The spermatheca is saclike and slightly enlarged at the proximal end of the ductus receptaculi, and composed of muscle sheath, basement membrane, epithelial cells and lumen. The female spermathecal accessory gland is located at the end of the spermatheca, and in the form of a uniform spiral tube mainly composed of muscle layer, epithelial cell layer and the central lumen of the accessory gland. 【Conclusion】 The reproductive system of female adult of *L. delicatula* is similar to those of the previously reported fulgoroid groups, but the number of ovarian tubules differs from those of other families. The morphological characteristics of female accessory glands and spermathecal gland differ among families in the suborder Auchenorrhyncha. The ultrastructure of *L. delicatula* is also somewhat different from that of the species in Cicadelloidea and Cercopoidea. Whether these differences can be used for the division of higher taxa of Auchenorrhyncha needs to be studied further.

Key words: Fulgoridae; *Lycorma delicatula*; female reproductive system; morphology; ultrastructure; transmission electron microscope

昆虫的生殖系统是昆虫繁殖后代、延续种族的器官,其构造和功能是研究昆虫生殖能力和适应性的基础,与昆虫种群数量的消长密切相关(彩万志等, 2001; 王荫长, 2004; Klowden, 2008)。研究昆虫生殖系统的超微结构特征,不仅可用于近缘类群的分类鉴定,还可以为系统发育关系探讨提供重要证据。

蜡蝉总科(Fulgoroidea)是半翅目(Hemiptera)头喙亚目(Auchenorrhyncha)中一个较大的类群,目前已记载约1 500属13 600多种,广泛分布于世界各大地理区(宋南和江志毅, 2012; Bourgoin, 2019)。该类群均为植食性,一些种类还可以传播植物病毒病,是农林业生产上的重要害虫(Yang *et al.*, 2015; Zhang *et al.*, 2019)。有关蜡蝉总科昆虫雌性生殖系统的整体形态和超微结构研究较少,目前仅见 Ammar (1985)研究了玉米花翅飞虱 *Peregrinus maidis* 卵巢的超微结构,在发育的卵母细胞中发现了类菌体;Bourgoin 和 Huang (1991)以及 Bourgoin (1993)明确了蜡蝉亚目昆虫雌性生殖系统的整体形态;Bourgoin 和 O'Brien (1994)研究了蜡蝉科中 *Odontoptera toulgoeti* 的雌性生殖系统,提供了内部结构形态图;D'Urso 等(2005)发现颖蜡蝉科中

Cixidia sikaniae 每个卵巢有6个卵巢管,卵巢管外有卵巢鞘;Michalik 等(2009)和 Szklarzewicz 等(2007)分别观察了脉菱蜡蝉 *Cixius nervosus*、古北飞虱 *Javesella pellucida* 和 *Conomelus anceps* 卵巢的超微结构,发现卵子发生早期的卵母细胞和滋养细胞位于滋养体底部,卵泡上皮细胞环绕卵母细胞排列;林江(2011)和林江等(2011)描述了缘蛾蜡蝉 *Salurnis marginella*、八点广翅蜡蝉 *Ricania speculum*、斑衣蜡蝉 *Lycorma delicatula* 和柿广翅蜡蝉 *Ricania sublimata* 雌性生殖系统,并提供了相应的形态特征图。此后,有关蜡蝉总科雌性生殖系统超微结构一直未见报道。

斑衣蜡蝉 *Lycorma delicatula* 隶属蜡蝉总科(Fulgoroidea)蜡蝉科(Fulgoridae)斑衣蜡蝉属 *Lycorma*,该种原记载于中国,后扩散至孟加拉国、印度、越南、日本、韩国等其他亚洲国家,主要危害观赏乔木和灌木等(Kim *et al.*, 2013; Yang *et al.*, 2014)。近年来还入侵北美,给当地的葡萄及果树产业带来严重为害(Barringer *et al.*, 2015; Dara *et al.*, 2015)。本研究采用光学显微镜和透射电子显微镜技术,观察斑衣蜡蝉的雌性生殖系统整体形态及超微结构,旨在明确其主要器官的超微结构特征,

为蜡蝉总科昆虫分类和交配机制研究提供更多的形态证据。

1 材料与方法

1.1 供试昆虫

斑衣蜡蝉 *L. delicatula* 成虫于 2018 年 9 月采自陕西杨陵 (34°29'32"N, 108°6'91"E), 采集的新鲜雌虫标本置于养虫笼内带回实验室迅速活体解剖。

1.2 光学显微镜观察

将活体雌成虫置于 2% 磷酸盐缓冲溶液 (phosphate buffered saline, PBS) (0.1 mol/L, pH 7.2) 的凹面载玻片上, 在体视显微镜 (型号: Jiangnan JSZ6) 下快速解剖出雌性生殖系统的交配囊、前阴道、后阴道、中输卵管、受精囊管、受精囊、卵巢和受精囊附腺等, 并移入滴有 2% 磷酸盐缓冲溶液的凹面皿中, 在光学显微镜 (型号: Leica M205 A) 下观察并拍照。

1.3 透射电子显微镜样品制备与观察

用尖头镊子将解剖并分离的雌性生殖系统各部分器官放入 2.5% 戊二醛的 2.0 mL 离心管中, 在 4℃ 冰箱中固定 12 h 后取出, 用 0.1 mol/L 的磷酸盐缓冲溶液 (pH 7.2) 漂洗 3 次, 每次 15 min; 于 1% 锇酸溶液 4℃ 条件下固定 2 h, 再用 0.1 mol/L 的磷酸盐缓冲溶液 (pH 7.2) 漂洗 3 次, 每次 10 min; 用梯

度乙醇 (体积比 30%, 50%, 70%, 80%, 90% 和 100%) 进行逐级脱水, 各浓度 2 次, 每次 8 min; 随后在 2.0 mL 离心管中用乙醇/伦敦白胶 (LR White 树脂) 混合物进行 3 次渗透 (3:1, 1:1 和 1:3, v/v), 时间分别为 2, 8 和 12 h, 再用纯伦敦白胶包埋剂渗透 2 次, 每次 24 h。将样品胶囊贴好标签放入包埋板内, 进行摇床震荡, 最后用纯伦敦白胶包埋剂进行包埋, 在 55℃ 烘箱内聚合 48 h。

将制作好的胶粒用修块机 (型号: Leica EM Trim2) 进行样品修整, 用 Leica EM UC7 型超薄切片机进行半薄定位和超薄切片 (厚度约为 75 nm), 置于 80 目的铜网上, 然后用醋酸铀和柠檬酸铅双重染色 (分别为 10 和 20 min), 在 TECNAI G2 SPIRIT BIO 型透射电子显微镜 80 kV 下进行观察和拍照, 获取的图片用 Adobe Photoshop CS6 进一步处理。

2 结果

2.1 雌性生殖系统整体形态

斑衣蜡蝉雌性生殖系统主要包括 1 对卵巢、1 个中输卵管、1 个交配囊、1 个交配囊管、1 个前阴道、1 个后阴道、1 个受精囊、1 个受精管和 2 根受精囊附腺 (图 1)。2 个卵巢发达对称, 呈端滋式。交配囊膨大呈长圆形, 下方连接交配囊管, 交配囊管再

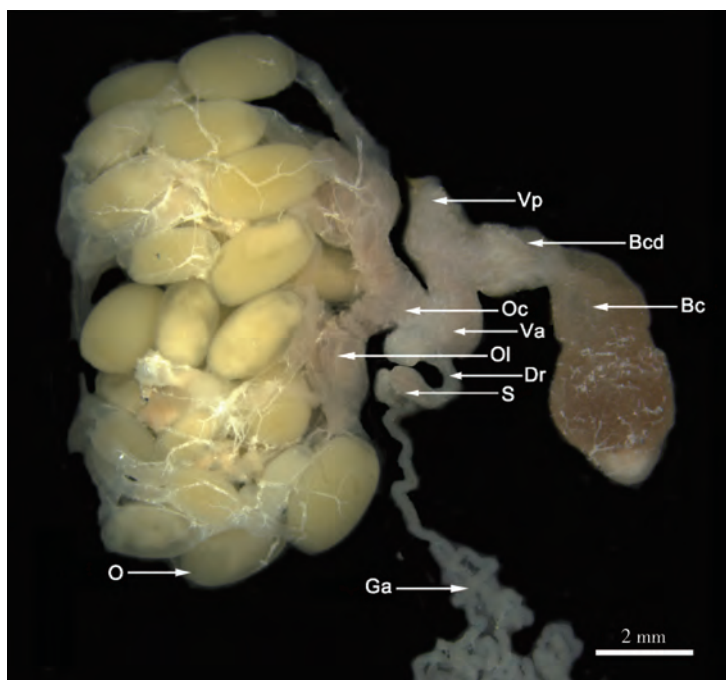


图 1 斑衣蜡蝉雌成虫生殖系统结构

Fig. 1 Structure of the reproductive system of female adult of *Lycorma delicatula*

Bc: 交配囊 Bursa copulatrix; Bcd: 交配囊管 Bursa copulatrix duct; Dr: 受精管 Ductus receptaculi; Ga: 受精囊附腺 Spermathecal accessory gland; O: 卵巢 Ovary; Oc: 中输卵管 Common oviduct; Ol: 侧输卵管 Lateral oviduct; S: 受精囊 Spermatheca; Va: 前阴道 Anterior vagina; Vp: 后阴道 Posterior vagina.

与后阴道相连。前阴道连接后阴道和受精管,受精囊管末端膨起形成椭圆状的受精囊,中输卵管开口于前阴道侧腹部,受精囊附腺细长管状,其一端着生在受精囊尾部,另一端附着在交配囊上。

2.2 雌性生殖系统超微形态

交配囊膨大呈圆球状。交配囊的囊壁由上皮细胞、肌肉层和基膜组成(图2:A)。肌肉层呈石块状整齐排列,上皮细胞核明显,具分泌颗粒,细胞层内有大量囊泡结构和少量的基膜内折(图2:A,B)。交配囊的囊腔中可见一些分泌物质和精子(图2:C,D)。

交配囊管呈圆柱状,连接交配囊和后阴道,由肌肉鞘、上皮细胞层和管腔组成,上皮细胞核突出,存在基膜内折,微气管连接细胞基膜(图3:A,B),肌肉鞘内有大量的囊泡结构(图3:C);横切图显示管壁内微绒毛密集(图3:D),分布有大量的线粒体和内质网结构(图3:E,F)。

后阴道位于交配囊管下方,圆管状,靠近上皮细

胞处的微气管结构连接细胞层(图4:A)。管腔内存在大量微绒毛,其边缘分布有分泌颗粒(图4:B);大量的分泌颗粒和线粒体环绕于上皮细胞核周围(图4:C,D)。后阴道由上皮细胞层、肌肉鞘和管腔构成(图4:D)。

前阴道与后阴道末端相连,管状,端部延伸至中输卵管。前阴道由肌肉鞘、基膜、上皮细胞层和管腔组成,微气管以基膜连接肌细胞层,并形成内折与肌肉鞘相连(图5:A,B);上皮细胞层内充满囊泡结构(图5:C),上皮细胞核周围环绕着大量的线粒体结构(图5:D)。

中输卵管位于前阴道侧腹部,由中输卵管腔、上皮细胞、肌肉鞘和基膜组成(图6:A);上皮细胞核周围存在大量线粒体结构,上皮细胞层内充满囊泡结构(图6:B,C);肌肉层厚且发达,管壁外有微气管,连接肌肉鞘和基膜(图6:D)。

受精管从中输卵管末端延伸至受精囊,上皮细

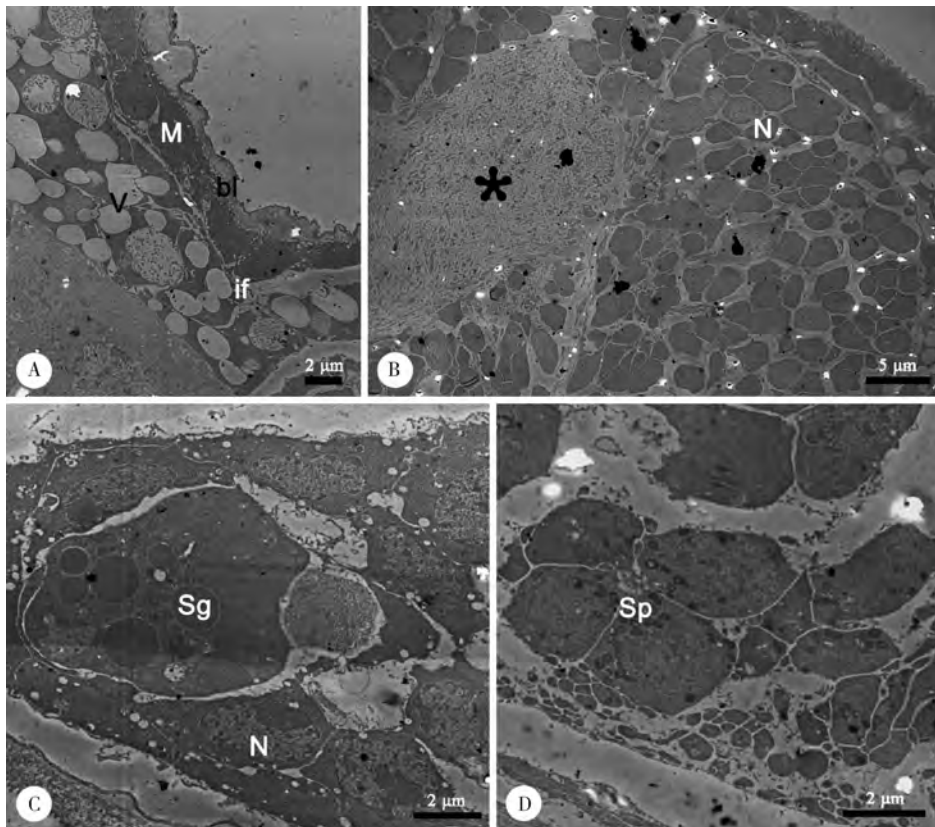


图2 斑衣蜡蝉雌成虫交配囊

Fig. 2 Bursa copulatrix of female adult of *Lycorma delicatula*

A: 交配囊横切,显示肌肉鞘(M)、基膜(bl)、大量的囊泡结构(V)和基膜内折(if) Cross section of bursa copulatrix, muscle sheath (M), basal lamina (bl), many vesicles (V) and basement membrane infolds (if); B: 囊腔中的分泌物(用星号指示) Secretion materials (indicated by an asterisk) in lumen; C, D: 显示分泌颗粒(Sg)和精子(Sp),以及上皮细胞核(N) Showing secretory granules (Sg) and spermatozoon (Sp), as well as epithelial nucleus (N).

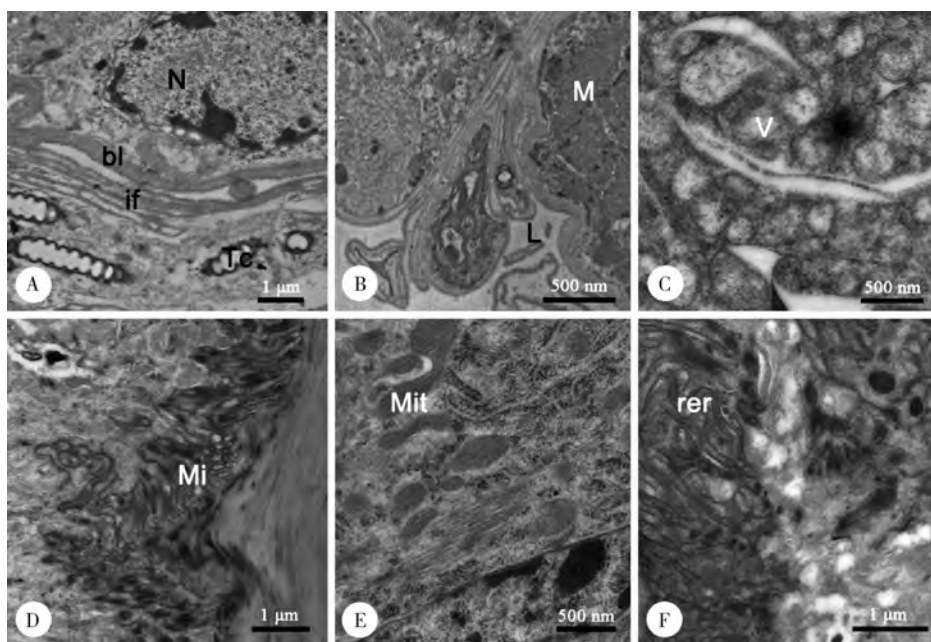


图3 斑衣蜡蝉雌成虫交配囊管

Fig. 3 Bursa copulatrix duct of female adult of *Lyrcorma delicatula*

A, B: 显示上皮细胞核(N)、基膜(bl)、基膜内折(if)、肌肉鞘(M)、管腔(L)和微气管(Tc) Showing epithelial nucleus (N), basal lamina (bl), basement membrane infolds (if), muscle sheath (M), lumen (L) and tracheoles (Tc); C: 显示大量的囊泡结构(V) Showing many vesicles (V); D, E, F: 交配囊管横切, 分别显示微绒毛(Mi)、线粒体(Mit)和内质网(rer) Cross section of bursa copulatrix duct, showing microvillus (Mi), mitochondria (Mit) and endoplasmic reticulum (rer), respectively.

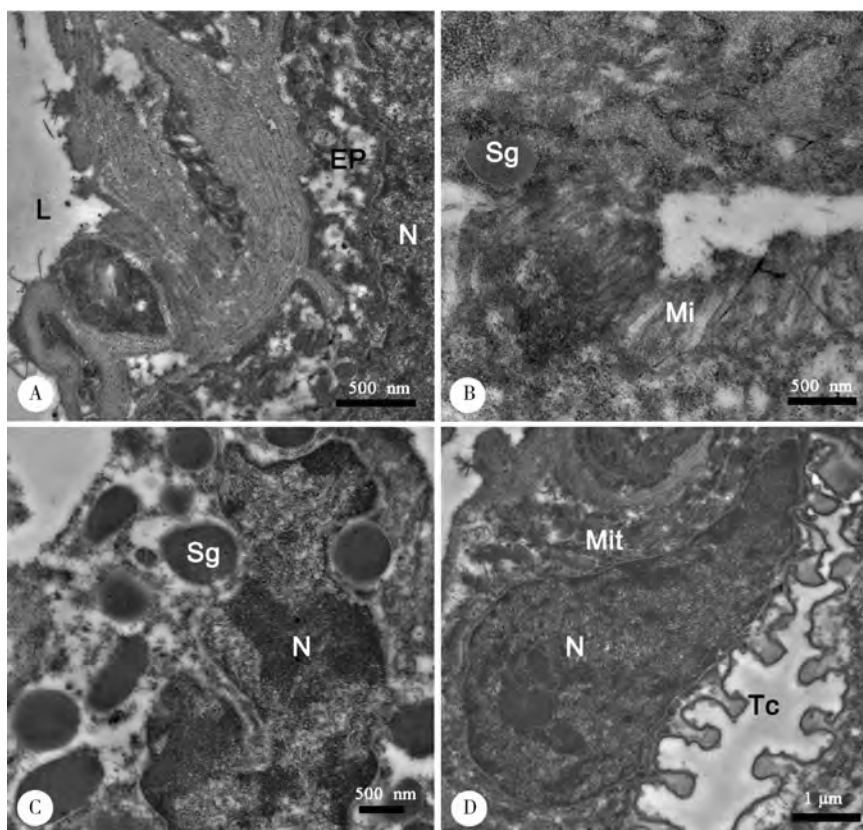


图4 斑衣蜡蝉雌成虫后阴道

Fig. 4 Posterior vagina of female adult of *Lyrcorma delicatula*

A: 后阴道横切, 显示管腔(L)、上皮细胞(EP)和细胞核(N) Cross section of posterior vagina, showing lumen (L), epithelial cell (EP) and nucleus (N); B, C: 显示微绒毛(Mi)和分泌颗粒(Sg), 以及上皮细胞核(N) Showing microvillus (Mi) and secretory granules (Sg), as well as epithelial nucleus (N); D: 显示上皮细胞核(N)、线粒体(Mit)和微气管(Tc) Showing epithelial nucleus (N), mitochondria (Mit) and tracheoles (Tc).

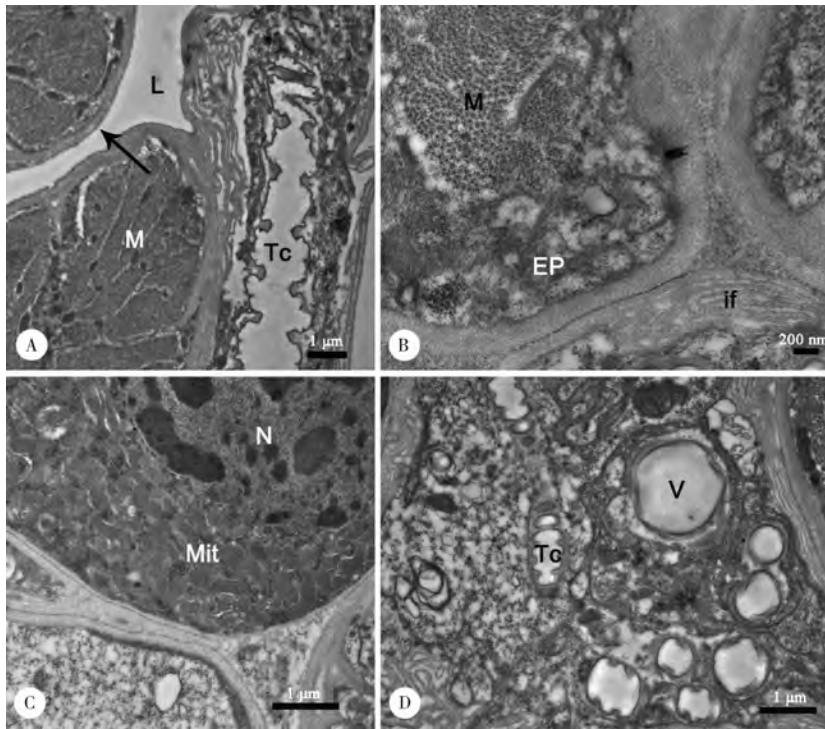


图5 斑衣蜡蝉雌成虫前阴道

Fig. 5 Anterior vagina of female adult of *Lycorma delicatula*

A: 前阴道横切,显示管腔(L)、肌肉鞘(M)和微气管(Tc),箭头指基膜 Cross section of anterior vagina, showing lumen (L), muscle sheath (M) and tracheoles (Tc), arrow indicating basement membrane; B: 前阴道纵切,显示肌肉鞘(M)、上皮细胞(EP)和基膜内折(if) Longitudinal section of anterior vagina, showing muscle sheath (M), epithelial cell (EP) and basement membrane infolds (if); C: 显示上皮细胞核(N)和线粒体(Mit) Showing epithelial nucleus (N) and mitochondria (Mit); D: 显示大量的囊泡结构(V)和微气管(Tc) Showing many vesicles (V) and tracheoles (Tc).

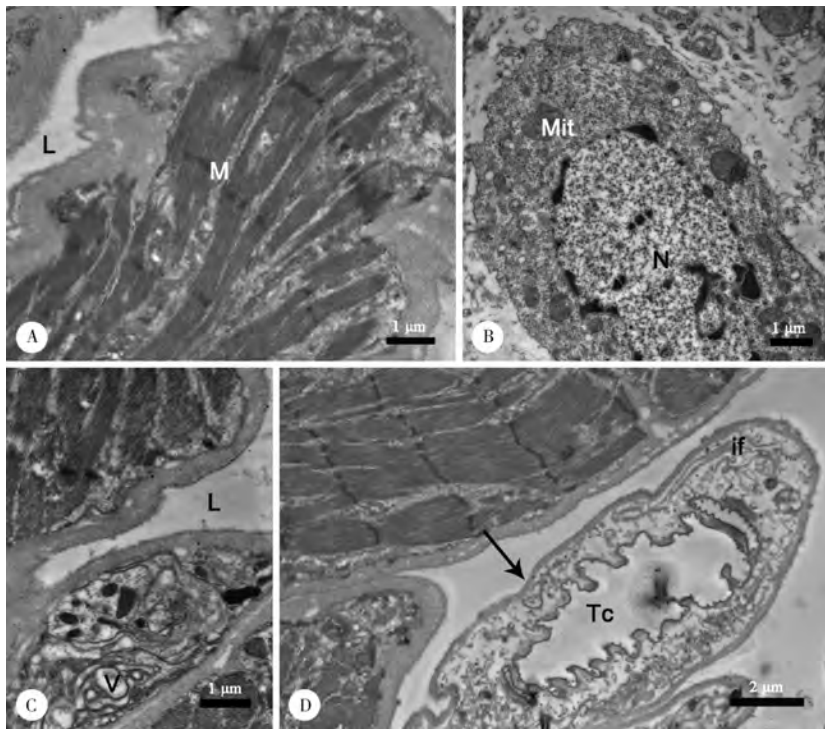


图6 斑衣蜡蝉雌成虫中输卵管

Fig. 6 Common oviduct of female adult of *Lycorma delicatula*

A: 中输卵管管壁横切,显示管腔(L)和肌肉鞘(M) Cross section of the common oviduct wall, showing lumen (L) and muscle sheath (M); B: 上皮细胞核(N)周围有大量的线粒体结构(Mit) Epithelial nucleus (N) is surrounded by numerous mitochondria (Mit); C: 显示大量的囊泡结构 Showing many vesicles (V); D: 显示基膜内折(if),以及微气管(Tc)连接基膜(箭头指示) Showing basement membrane infolds (if), and the tracheole (Tc) connecting with basal lamina (indicated by an arrow).

胞间有少量的基膜内折(图 7: A);肌细胞间隙明显且边界清楚,存在囊泡结构(图 7: B);管腔内有大量层状内质网和线粒体结构,以及一些腔内分泌物(图 7: C);肌细胞交错排列,存在层状体(图 7: D),受精管壁由基膜、厚层肌肉鞘和管腔组成(图 7: E)。

受精囊为受精管近末端略膨大的囊状结构,由肌肉鞘、基膜、上皮细胞和囊腔构成,囊壁由较厚的肌肉层组成(图 8: A, B)。肌肉鞘细胞间由微气管相连,靠近管腔处为上皮细胞层(图 8: A, B);上皮细胞层边缘环绕大量微绒毛,内部布满线粒体和内质网结构(图 8: C, D)。受精囊腔中散布大量精子结构和角质层(图 8: E)。

卵室由固有膜、滤泡细胞和卵细胞组成(图 9: A, B)。中下部的滋养细胞中有合胞体(图 9: C),其细胞核又分化为滋养细胞和卵母细胞的细胞核。卵室内充满形状不规则的滋养细胞,细胞周围存在内共生细菌(图 9: C, D)。卵细胞间存在细胞间隙,细胞核外分布着大量线粒体和内质网结构(图 9: E)。

受精囊附腺着生于受精囊末端,为均匀的螺旋管状,主要由肌肉层、上皮细胞层和中心管腔组成(图 10: A);上皮细胞层内有大量的内质网和圆形分泌颗粒(图 10: B),受精囊附腺管腔内基膜内折,有囊泡结构(图 10: C);分泌细胞前体物质外围环绕一些颗粒物,内部主要是丝状物质(图 10: D)。

3 讨论

斑衣蜡蝉与蜡蝉总科(Fulgoroidea)中其他已报道类群的雌性生殖系统结构相似,均由卵巢、中输卵管、交配囊、交配囊管、前阴道、后阴道、受精囊、受精管和受精囊附腺等部分构成,但不同类群的卵巢小管数目存在差异,如:中华彩象蜡蝉 *Dictyophara sinica* [隶属象蜡蝉科(Dictyopharidae)] 的卵巢有 6 个卵巢小管,缘蛾蜡蝉 *S. marginella* [隶属蛾蜡蝉科(Flatidae)] 有 8 个卵巢小管,山东宽广蜡蝉 *Pochazia shantungensis*、八点广翅蜡蝉 *R. speculum*、透明疏广蜡蝉 *Euricania clara* [隶属广蜡蝉科(Ricaniidae)] 有 12 个卵巢小管(林江, 2011)。本研究观察到斑衣蜡蝉的卵巢由 14 个卵巢小管组成。可见,雌性生殖系统卵巢小管数目在不同科间有差异。林江(2011)和林江等(2011)观察了斑衣蜡蝉的雌性生殖系统整体结构,本文为了全面起见,也提

供了该种雌性生殖系统的整体形态特征图。在此基础上,本研究首次对卵巢、中输卵管、交配囊、交配囊管、前阴道、后阴道、受精囊、受精管和受精囊附腺的超微结构进行了观察和描述。

根据现有研究,半翅目头喙亚目中叶蝉总科(Cicadelloidea)和蝉总科(Cicadoidea)昆虫中输卵管膨大,受精囊及交配囊呈圆形或椭圆形,精子储存在受精囊内(Bourgoin, 1993; Hayashi and Kamimura, 2002; Hummel *et al.*, 2006; 苏梅, 2014);沫蝉总科(Cercopoidea)昆虫中输卵管中部略微膨起形成交配囊,受精囊退化,精子储存在交配囊中(王婷婷, 2015);角蝉总科(Membracoidea)昆虫中输卵管基部着生膨大的受精囊,交配囊退化(钟海英, 2014)。蜡蝉总科昆虫的中输卵管短粗,开口于前阴道,下方连接 2 根侧输卵管,交配囊位于后阴道背面,受精囊位于受精囊管近末端,用于储存精子(Bourgoin, 1993)。本研究发现斑衣蜡蝉的中输卵管、交配囊及受精囊与林江(2011)和林江等(2011)有关广蜡蝉科(Ricaniidae)、蛾蜡蝉科(Flatidae)和象蜡蝉科(Dictyophoridae)代表种类的中输卵管、交配囊及受精囊的形态结构相似,而不同于蝉总科、叶蝉总科和沫蝉总科的种类。这是否是蜡蝉总科昆虫的独有特征需要进一步研究。此外,本研究观察的斑衣蜡蝉受精囊壁的超微结构以及在囊腔内发现单个游离精子,与叶蝉总科和蝟蛉科昆虫 *Panorpa sexspinosa* 和 *Panorpa jilinensis* 受精囊壁的组成和囊内的精子分布状态相似(Hayashi and Kamimura, 2002; 马娜, 2012; 苏梅, 2014),进一步证实了受精囊为昆虫储存精子的重要场所。斑衣蜡蝉交配囊内存在游离精子和分泌物质,说明交配囊是雌雄虫交配的场所,雄虫的精子在交配囊中短暂贮存及活化,这与已报道的头喙亚目昆虫以及其他类群交配囊结构功能一致(Hayashi and Kamimura, 2002; Hummel *et al.*, 2006; 王婷婷, 2015)。

雌性昆虫常具雌性附腺和受精囊附腺(Leopold and Degrugillier, 1973; Leopold *et al.*, 1978; Degrugillier, 1985; 彩万志等, 2001)。半翅目头喙亚目中叶蝉总科和沫蝉总科雌成虫雌性附腺为 1 根粗细均匀的管状结构,与交配囊相连,受精囊附腺不发达(苏梅, 2014; 王婷婷, 2015);蝉总科雌成虫雌性附腺着生于侧输卵管基部,受精囊附腺极长(钟海英, 2014);角蝉总科雌成虫雌性附腺 2 根,粗长,受精囊附腺 1 根,基半部细于端半部(Tsai and Perrier, 1996; 钟海英, 2014)。本研究中斑衣蜡蝉

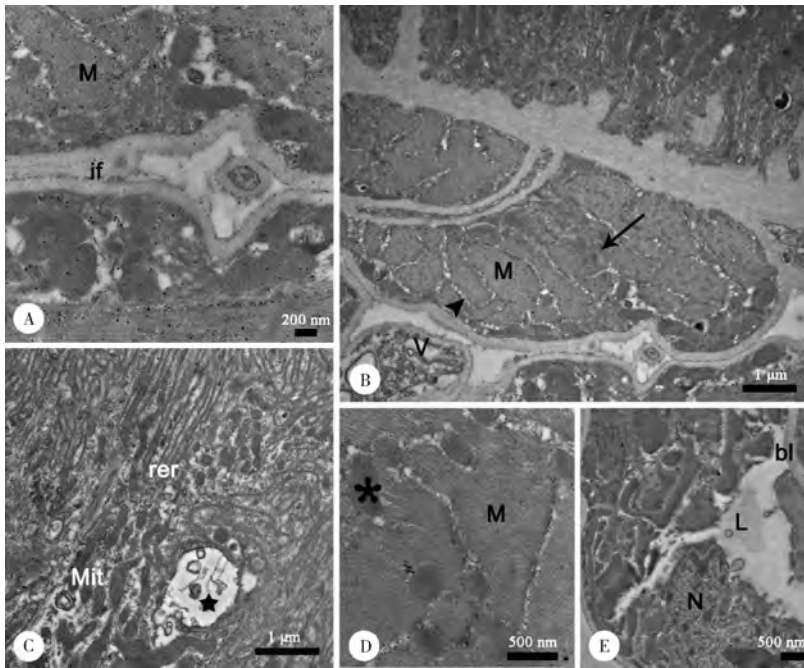


图7 斑衣蜡蝉雌成虫受精管

Fig. 7 Ductus receptaculi of female adult of *Lycorma delicatula*

A, B: 受精管横切,显示肌肉鞘(M)、囊泡结构(V)和基膜内折(if),三角箭头指肌细胞间边界,箭头指肌细胞连接线 Cross section of ductus receptaculi, showing muscle sheath (M), vesicles (V) and basement membrane infolds (if), triangular arrow indicating muscle cell limit, and arrow indicating tight junction between muscle cells; C: 显示大量线粒体(Mit)、内质网(rer)和腔内分泌物(用五角星指示) Showing many mitochondria (Mit), endoplasmic reticulum (rer) and secretory granules in lumen (indicated by an asterisk); D, E: 显示受精管管腔(L)、上皮细胞核(N)、基膜(bl)、肌肉鞘(M)和层状体(用星号指示),以及肌细胞排列 Showing lumen of ductus receptaculi (L), epithelial nucleus (N), basal lamina (bl), muscle sheath (M) and lamellar structure (indicated by an asterisk), and the arrangement of muscle cells.

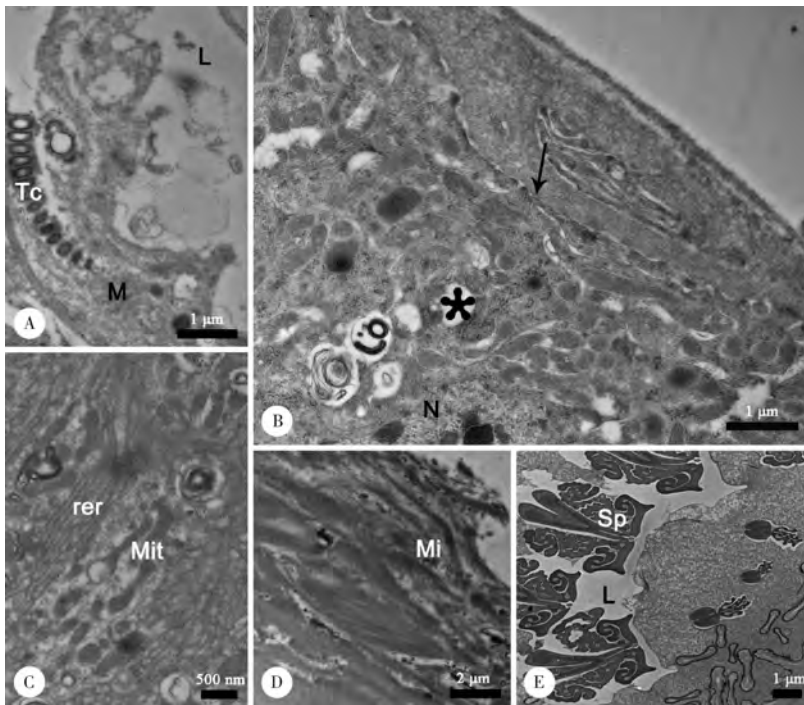


图8 斑衣蜡蝉雌成虫受精囊

Fig. 8 Spermatheca of female adult of *Lycorma delicatula*

A: 受精囊纵切,显示囊腔(L)、肌肉鞘(M)和微气管(Tc) Longitudinal section of spermatheca, showing lumen (L), muscle sheath (M) and tracheoles (Tc); B: 显示上皮细胞核(N)和腔内分泌物(用星号指示),箭头指细胞边界 Showing epithelial nucleus (N) and secretory granules in lumen (indicated by an asterisk), arrow indicating cell limit; C, D: 显示大量线粒体(Mit)、内质网(rer)和微绒毛(Mi) Showing many mitochondria (Mit), endoplasmic reticulum (rer) and microvillus (Mi); E: 显示囊腔(L)内大量精子(Sp) Showing numerous sperm (Sp) in lumen (L).

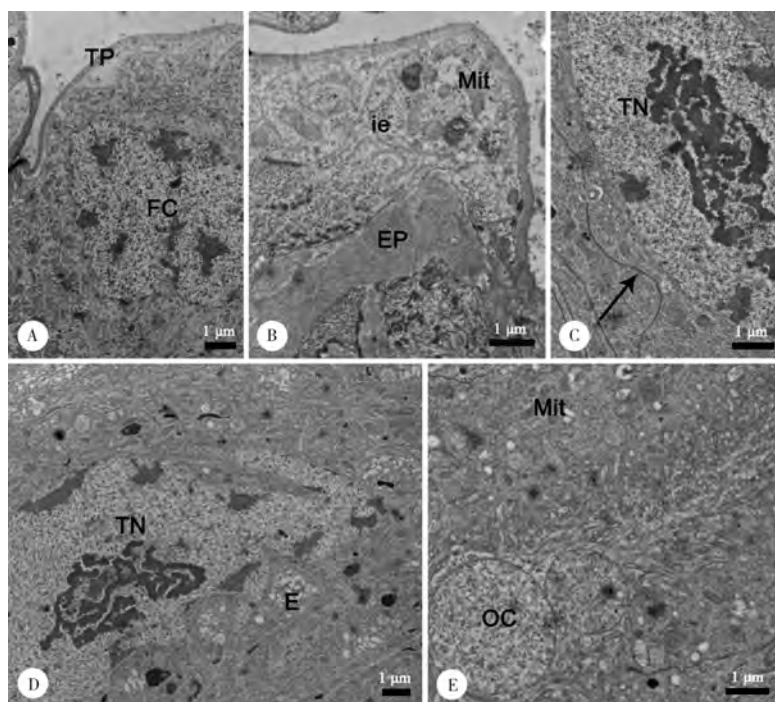


图9 斑衣蜡蝉雌成虫卵巢

Fig. 9 Ovary of female adult of *Lycorma delicatula*

A, B: 卵巢管横切, 显示卵巢的固有膜 (TP)、滤泡细胞 (FC) 和上皮细胞 (EP), 胞质中存在大量线粒体 (Mit), 细胞间隙 (ie) 明显 Cross section of ovary, showing tunica propria (TP), follicular cells (FC) and epithelium cell (EP). Lots of mitochondria (Mit) exist in the cytoplasm. Intercellular spaces (ie) in the follicular epithelial cells are obvious; C, D: 显示滋养细胞核 (TN) 和内共生细菌 (E) 在 germarium, 箭头指合胞体膜 Showing trophocyte nucleus (TN) and endosymbiotic bacteria (E) in germarium, arrow indicating membranes of the syncytial lobes; E: 显示卵母细胞 (OC) 和线粒体 (Mit) Showing oocytes (OC) and mitochondria (Mit).

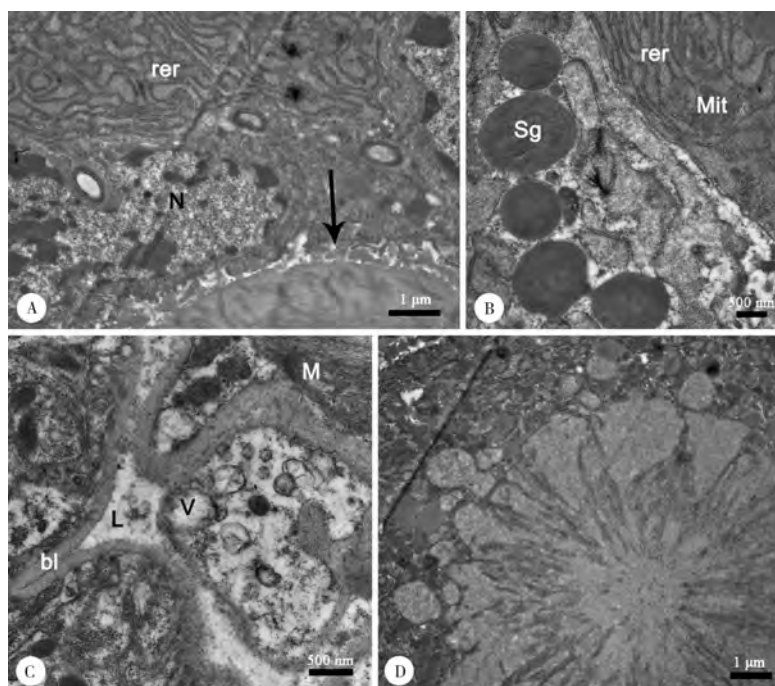


图10 斑衣蜡蝉雌成虫受精囊附腺

Fig. 10 Spermathecal accessory gland of female adult of *Lycorma delicatula*

A, C: 受精囊附腺壁横切, 显示上皮细胞核 (N)、管腔 (L)、囊泡 (V)、内质网 (rer)、肌肉鞘 (M) 和基膜 (bl), 箭头指细胞连接 Cross section of spermathecal accessory gland wall, showing epithelial nucleus (N), lumen (L), vesicles (V), endoplasmic reticulum (rer), muscle sheath (M) and basal lamina (bl), arrow indicating connections between cells; B: 受精囊附腺的分泌颗粒物质 (Sg), 以及周围的内质网结构 (rer) 和线粒体 (Mit) Secretory granules of spermathecal accessory gland (Sg), and the surrounding endoplasmic reticulum (rer) and mitochondria (Mit); D: 分泌细胞前体物质横切, 显示内层丝状物和外层颗粒物 Cross section of secretion of cellular precursors, showing inner filaments and outer particles.

受精囊附腺为 2 根螺旋管, 连接在受精囊末端, 附着在交配囊上, 雌性附腺结构退化, 这与蜡蝉总科中颖蜡蝉科 (Achilidae)、蜡蝉科 (Fulgoridae)、广蜡蝉科 (Ricanidae)、蛾蜡蝉科 (Flatidae) 及象蜡蝉科 (Dictyopharidae) 雌成虫雌性附腺和受精囊附腺的结构组成 (Bourgoin, 1993; Bourgoin and O'Brien, 1994; D'Urso *et al.*, 2005; 林江, 2011) 一致。可见头喙亚目中不同总科雌成虫雌性附腺与受精囊附腺的形态特征存在明显区别。这些形态特征差异是否可以作为该亚目高级阶元划分的依据, 仍有待进一步探讨。

在雌性生殖系统超微结构方面, 本研究观察的斑衣蜡蝉中输卵管由中输卵管腔、上皮细胞、肌肉鞘和基膜组成, 且肌肉层发达, 这与叶蝉总科中黑尾叶蝉 *Bothrogonia ferruginea*、玻璃叶蝉 *Homalodisca coagulata*、横线叶蝉 *Exitianus nanus*、条沙叶蝉 *Psammotettix striatus* 和槭锥顶叶蝉 *Japananus hyalinus* 中输卵管的超微结构 (Hayashi and Kamimura, 2002; Hummel *et al.*, 2006; 苏梅, 2014) 大体一致, 但斑衣蜡蝉中输卵管上皮细胞层内未发现微绒毛和分泌颗粒; 此外, 斑衣蜡蝉交配囊囊壁由上皮细胞、肌肉层和基膜组成, 上皮细胞层内有囊泡和基膜内折, 这与沫蝉总科中牧草长沫蝉 *Philaenus spumarius*、陕西尖胸沫蝉 *Aphrophora shaanxiensis* 和四斑象沫蝉 *Philagra quadrimaculata* 交配囊结构 (王婷婷, 2015) 相似, 但上皮细胞层中未发现黑色颗粒物。斑衣蜡蝉与其他头喙亚目昆虫雌性生殖系统超微结构是否还存在更多差异, 也需要进一步深入研究。

参考文献 (References)

- Ammar ED, 1985. Internal morphology and ultrastructure of leafhoppers and planthoppers. In: Nault LR, Rodriguez JG eds. *The Leafhoppers and Planthoppers*. Wiley, New York. 127 – 162.
- Barringer LE, Donovall LR, Spichiger SE, Lynch D, Henry D, 2015. The first new world record of *Lycorma delicatula* (Insecta: Hemiptera: Fulgoridae). *Entomol. News*, 125(1): 20 – 23.
- Bourgoin T, 1993. Female genitalia in Hemiptera Fulgoromorpha, morphological and phylogenetical data. *Ann. Soc. Entomol. Fr.*, 29(3): 225 – 244.
- Bourgoin T, 2019. FLOW (Fulgoromorpha Lists on the Web) [EB/OL], Version 8. <http://hemiptera-databases.org/flow/>.
- Bourgoin T, Huang J, 1991. Comparative morphology of female genitalia and the copulatory mechanism in Trypetimorphini (Hemiptera, Fulgoromorpha, Tropicuchidae). *J. Morphol.*, 207(2): 149 – 155.
- Bourgoin T, O'Brien L, 1994. Review of the genus *Odontoptera* Carreño (Homoptera: Fulgoridae) with description of a new species. *Ann. Entomol. Soc. Am.*, 87(5): 516 – 522.
- Cai WZ, Hua BZ, Pang XF, 2001. *General Entomology*. China Agricultural University Press, Beijing. [彩万志, 花保祯, 庞雄飞, 2001. 普通昆虫学. 北京: 中国农业大学出版社]
- D'Urso V, Guglielmino A, Mauceci A, 2005. The internal male and female reproductive apparatus in *Cixidia sikaniae* D'Urso & Guglielmino, 1995 (Fulgoromorpha: Achilidae). *Zootaxa*, 1077: 25 – 36.
- Dara SK, Barringer L, Arthurs SP, 2015. *Lycorma delicatula* (Hemiptera: Fulgoridae): a new invasive pest in the United States. *J. Integr. Pest Manag.*, 6(1): 1 – 6.
- Degrugillier ME, 1985. *In vitro* release of housefly *Musca domestica* L. (Diptera: Muscidae), acrosome material after treatment with secretion of female accessory gland and micropyle cap substance. *Int. J. Insect Morphol. Embryol.*, 14(6): 381 – 391.
- Hayashi F, Kamimura Y, 2002. The potential for incorporation of male derived proteins into developing eggs in the leafhopper *Bothrogonia ferruginea*. *J. Insect Physiol.*, 48(2): 153 – 159.
- Hummel NA, Zalom FG, Peng CYS, 2006. Anatomy and histology of reproductive organs of female *Homalodisca coagulata* (Hemiptera: Cicadellidae: Proconiini), with special emphasis on categorization of vitellogenic oocytes. *Ann. Entomol. Soc. Am.*, 99(5): 920 – 932.
- Kim H, Kim M, Kwon DH, Park S, Lee Y, Huang J, Kai S, Lee H, Hong K, Jang Y, Lee S, 2013. Molecular comparison of *Lycorma delicatula* (Hemiptera: Fulgoridae) isolates in Korea, China, and Japan. *J. Asia-Pac. Entomol.*, 16: 503 – 506.
- Klowden MJ, 2008. *Physiological Systems in Insects*. 2nd ed. Science Press, Beijing, China. 181 – 223.
- Leopold RA, Degrugillier ME, 1973. Sperm penetration of housefly eggs: evidence for involvement of female accessory secretion. *Science*, 181(4099): 555 – 557.
- Leopold RA, Meola S, Degrugillier ME, 1978. The egg fertilization site within the housefly, *Mosca domestica* L. (Diptera: Muscidae). *Int. J. Insect Morphol. Embryol.*, 7(2): 111 – 120.
- Lin J, 2011. *Biology of Ricania sublimata and Morphology Compared with Other Related Species* (Hemiptera: Fulgoroidea). MSc Thesis, Northwest A&F University, Yangling, Shaanxi. [林江, 2011. 柿广翅蜡蝉生物学及其相近种类的形态学比较研究. 陕西杨凌: 西北农林科技大学硕士学位论文]
- Lin J, Zhang YL, Wang YL, 2011. A comparative study on the female reproductive system of four species of the Fulgoroidea (Hemiptera). *Acta Zootax. Sin.*, 36(3): 689 – 701. [林江, 张雅林, 王应伦, 2011. 四种蜡蝉雌性生殖系统比较研究(半翅目, 蜡蝉总科). 动物分类学报, 36(3): 689 – 701]
- Ma N, 2012. *The Female Reproductive System Structure, Copulatory Mechanism and Phylogenetic Analysis of Panorpidae* (Mecoptera). PhD Dissertation, Northwest A&F University, Yangling, Shaanxi. [马娜, 2012. 蝎蛉科昆虫雌性生殖系统结构、交配机制和系统发育研究(长翅目). 陕西杨凌: 西北农林科技大学博士学位论

文]

- Michalik A, Jankowska W, Szklarzewicz T, 2009. Ultrastructure and transovarial transmission of endosymbiotic microorganisms in *Conomelus anceps* and *Metcalfa pruinosa* (Insecta, Hemiptera, Fulgoromorpha). *Folia Biol. (Krakow)*, 57(3-4): 131-137.
- Song N, Jiang ZY, 2012. Studies on systematics of Fulgoroidea (Insecta: Hemiptera). *Sichuan J. Zool.*, 31(2): 317-322. [宋南, 江志毅, 2012. 蜡蝉总科(昆虫纲: 半翅目) 系统分类研究进展. *四川动物*, 31(2): 317-322]
- Su M, 2014. Morphology and Ultrastructure of the Reproductive System in Deltocephalinae. MSc Thesis, Northwest A&F University, Yangling, Shaanxi. [苏梅, 2014. 角顶叶蝉亚科昆虫生殖系统的形态及超微结构研究. 陕西杨凌: 西北农林科技大学硕士学位论文]
- Szklarzewicz T, Jankowska W, Lukasiewicz K, Szymańska B, 2007. Structure of the ovaries and oogenesis in *Cixius nervosus* (Cixiidae), *Javesella pellucida* and *Conomelus anceps* (Delphacidae) (Insecta: Hemiptera: Fulgoromorpha). *Arthropod Struct. Dev.*, 36(2): 199-207.
- Tsai JH, Perrier JL, 1996. Morphology of the digestive and reproductive systems of *Dalbulus maidis* and *Graminella nigrifrons* (Homoptera: Cicadellidae). *Fla. Entomol.*, 79: 563-578.
- Wang TT, 2015. Morphology and Ultrastructure of the Reproductive System in Aphrophoridae. MSc Thesis, Northwest A&F University, Yangling, Shaanxi. [王婷婷, 2015. 尖胸沫蝉科昆虫生殖系统的形态及超微结构研究. 陕西杨凌: 西北农林科技大学硕士学位论文]
- Wang YC, 2004. Insect Physiology. Agricultural Press, Beijing. [王荫长, 2004. 昆虫生理学. 北京: 农业出版社]
- Yang Z, Wang XY, Kim JH, 2014. Parasitism rate of egg parasitoid *Anastatus orientalis* (Hymenoptera: Eupelmidae) on *Lycorma delicatula* (Hemiptera: Fulgoridae) in China. *Korean J. Appl. Entomol.*, 53(2): 135-139.
- Yang ZQ, Choi WY, Cao LM, Wang XY, Hou ZR, 2015. A new species of *Anastatus* (Hymenoptera: Eupelmidae) from China, parasitizing eggs of *Lycorma delicatula* (Homoptera: Fulgoridae). *Zool. Syst.*, 40(3): 290-302.
- Zhang L, Zhao WH, Wang FP, Qin DZ, 2019. Genetic diversity and population structure of natural *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) populations in China as revealed by microsatellite and mitochondrial markers. *Insects*, 10(10): 312.
- Zhong HY, 2014. Comparative Morphology of the Digestive, Excretory and Reproductive Systems in Auchenorrhyncha (Insecta: Hemiptera). PhD Dissertation, Northwest A&F University, Yangling, Shaanxi. [钟海英, 2014. 头喙亚目昆虫消化、排泄及生殖系统的比较形态学研究(昆虫纲: 半翅目). 陕西杨凌: 西北农林科技大学博士学位论文]

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