



## 小综述

Mini-Review

### 小综述: 小菜蛾(*Plutella xylostella*)分子档案

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**摘要** 小菜蛾属于鳞翅目菜蛾科菜蛾属, 学名为 *Plutella xylostella* (L.) 英文名: Diamondback moth (DBM), 是鳞翅目昆虫中一个原始的类型。小菜蛾自身高度杂合, 有 31 条染色体 ( $n=31$ ), 基因组大小约为 343 Mb, 预测含有 18 071 个蛋白编码蛋白, 781 个非编码 RNA, 基因组中有 33.97% 重复序列组成, 小菜蛾拥有 1 412 个特有基因。小菜蛾基因组中存在丰富的 SNP、插入缺失、结构变异以及复合片段重复等 DNA 变异。小菜蛾大约在 124 万年以前与其它两个鳞翅目昆虫, 家蚕 (*B. mori*) 和 黑脉金斑蝶 (*D. plexippus*) 中分化出来。DBM 适应了各种环境的挑战, 这种对外界环境的适应与小菜蛾在幼虫阶段偏好表达的基因, 发现与气味感受、食物消化和解毒代谢相关的基因所构成的复杂基因网络密切相关。尤其是小菜蛾在长期进化过程中形成生物解毒代谢途径, 使得小菜蛾拥有对很多化学物质具有解毒能力, 从而使其成为一个臭名昭著的鳞翅目害虫。

**关键词** 小菜蛾; 基因组; 分子变异; 分子进化; 分子适应

### A Mini-review: Molecular Profile of Diamondback Moth (*Plutella xylostella*)

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**Abstract** Diamondback moth (DBM) belongs to Lepidoptera (Order), Plutellidae (Family), *Plutella* (Genus), its binomial name is *Plutella xylostella* (L.), which is deemed to be a basal and primitive lepidopteran insect as well as a high heterozygous insect. Diamondback moth has 31 chromosomes ( $n = 31$ ) and its genome size is about 343Mb, containing 18,071 protein-coding genes and 781 non-coding RNAs, with 33.97% of the genome made up of repetitive sequence. Diamondback moth has 1412 *P. xylostella* - unique genes. There are abundant DNA variations in genome such as SNPs, InDels, structural variations and complex segmental duplication patterns. Diamondback moth diverged about 124 million years ago from two other lepidopterans *B. mori* and *D. plexippus*. DBM adapts to a variety of environmental challenges, The abilities of these adaptations are closely related to a set of genes preferentially expressed at the larval stage that contribute to odorant chemoreception, food digestion and metabolic detoxification, particularly, in the long-term evolutionary DBM is evolved a biological detoxification pathway, developing the ability to detoxify many chemicals and *Bt* toxins, thus making it a notorious lepidopteran pests.

**Keywords** Diamondback moth (DBM); *Plutella xylostella* (L.); Genome; Molecular variation; Molecular evolution; Molecular adaptation

小菜蛾属于鳞翅目 (Lepidoptera) 菜蛾科 (Plutellidae) 菜蛾属, 学名为 *Plutella xylostella* (L.);

小菜蛾因其雄性成虫的前翅边缘有一系列的黄色波纹, 当蛾子翅膀收叠起来时, 这些图案叠加在一起在背上形成三个黄色钻石图案而得名为 Diamondback moth (DBM) (Ankersmit et al. 1953)。

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小菜蛾是以十字花科植物为食的昆虫, 由于其对重要的十字花科作物带来毁灭性的危害, 以及对化学农药及生物农药产生抗药性, 成为鳞翅目昆虫中最引人关注的农业害虫之一(Talekar N.S., & Shelton A.M., 1993; Furlong et al., 2012)

随着现代生物技术的迅速发展, 在分子水平上研究小菜蛾生物学特性成为研究热点, 在基因组学、分子遗传、分子进化以及分子适应方面取得了显著的进展(Xie, 2013)。

### 1 小菜蛾的基因组

小菜蛾的基因组大小约为 343 Mb, 预测含有 18,071 个蛋白编码蛋白, 781 个非编码 RNA, 基因组中有 33.97%重复序列组成(You et al., 2013)。小菜蛾拥有 1,412 个特有基因, 这些特有基因大都参与与环境信息处理、染色体复制或修复、转录调节以及碳水化合物、蛋白质代谢等基本的生物学途径(You et al., 2013)。

### 2 小菜蛾的分子遗传

小菜蛾自身高度杂合, 有 31 条染色体( $n=31$ ), 存在丰富的 SNP、插入缺失、结构变异以及复合片段重复等 DNA 变异(图 1)(You et al., 2013)。Baxter et al.利用下一代 RAD 测序技术构建了小菜蛾的连锁图谱 (Baxter et al., 2011B)。将 3,177 个母校遗传的 RAD 归属到 31 个染色体上, 使得能够鉴定农药抗性和 W/Z 性染色体; 用来自回交父本的 2,878 个分离的等位基因座构建了 1292 cM 长的基因组连锁图 (图 2)。同年, Baxter 还报道了一个膜转运子 (ABCC2)的基因座遗传定位, 这个基因座控制着两个鳞翅目昆虫的 Cry1Ac 毒蛋白抗性, 说明这个蛋白在 Bt 功能上起着关键的作用(Baxter et al., 2011A)。

### 3 小菜蛾的分子进化

小菜蛾是动物界、节肢动物门、昆虫纲、鳞翅目、菜蛾科、菜蛾属一种昆虫。小菜蛾大约在 124 万年以前与其它两个鳞翅目昆虫, 家蚕 (*B. mori*) 和黑脉金斑蝶 (*D. plexippus*) 中分化出来。利用现有昆虫基因组信息构建系统发育树证实小菜蛾属于鳞翅目昆虫中一个原始的类型(You et al., 2013)。系统发生分析确认昆虫目的分化时间大概在

265~332 万年以前, 这与单子双子叶植物分化时间为 304 万年以前相一致, 证实了昆虫行为与宿主植物存在共进化。当十字花科植物从番木瓜科 *caricaceae* 分化出来时 (54~90 万年以前), 小菜蛾即成为十字花科植物专食昆虫。

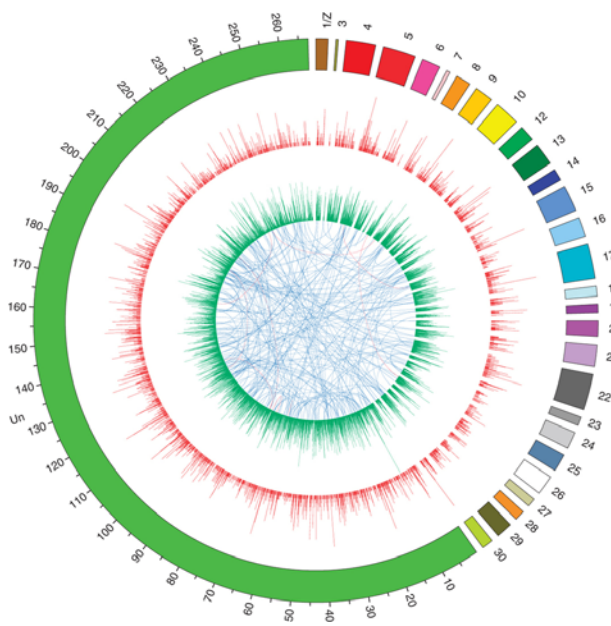


图 1 测序小菜蛾 (*P. xylostella*) 中的基因组变异(摘自: You et al., 2013)

注: 最外面的圆圈表示用 100 kb 单位尺度装配的参照基因组; 能被指派到连锁群的 Scaffolds 以随机顺序组合产生 28 个染色体的部分序列; 绿色的部分表示这些 Scaffolds 不能被指派(Un); 最里面的圆环表示大于 8kb 的片段重复, 连接线表示原始片段和副本位置; 100%相似性的片段重复用红色表示, 大于 90%相似性的片段用蓝色表示; 柱状图则分别表示单核苷多态性(SNPs)的数量(红色, 外圆)以及在 30 kb 和 50 kb 范围中的插入和缺失(Indels)(浅绿色, 内圆)

Figure 1 Genomic variations within the sequenced *P. xylostella* strain (Adopted from You et al. 2013)

Note: The outermost circle shows the reference genome assembly with a 100-kb unit scale. Scaffolds that could be assigned to linkage groups are joined in arbitrary order to generate the partial sequences of 28 chromosomes. The green segment represents the scaffolds that were unable to be assigned (Un). The innermost circle denotes segmental duplications ( $of \geq 8$  kb), with connections shown between segment origins and duplication locations. Segmental duplication pairs with 100% similarity are shown in red, and those with  $\geq 90\%$  similarity are shown in blue. Histograms indicate the number of SNPs (red, outer circle) and indels (light green, inner circle) in 30-kb and 50-kb windows, respectively

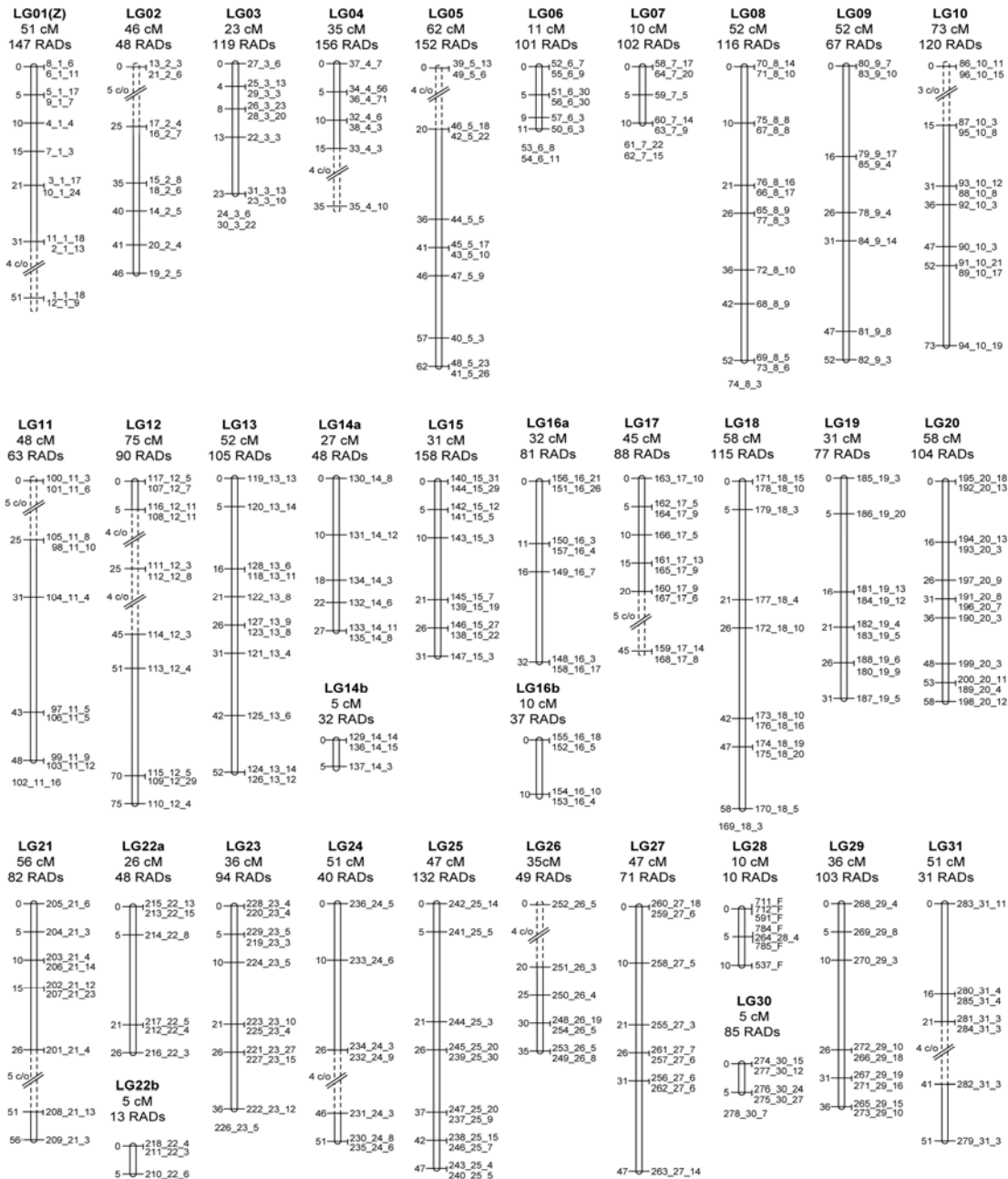


图 2 小菜蛾 (n=31) 基因组连锁图 (摘自: Baxter et al., 2011B)

注: 本图通过 2878 个分离的等位基因构建基因连锁图。每个连锁群包含 10~158 个 RAD 等位基因, 图谱总长为 1292 cM。每个 RAD 标记都用三个数字 (i ii iii) 来标识, 相对应为, i 表示 RAD 标记(1-285), ii 表示染色体数(1-31), iii 表示标记中 RAD 等位基因数。连锁群 1-28 与 *B. Mori* (n=28) 染色体编号系统同源, LG29, LG30 和 LG31 分别代表在 *B. Mori* 中与染色体 11, 23 和 24 的融合。图中虚线表示根据因太小而未分组的 3, 4 或 5 基因型差异推测出的连锁群。由于有 20 后代个体用于构建此图, 每个交叉的大概距离为 5 cM。在染色体 14, 16 和 22 上, 标记形成了两个明显的组, 因高重组率或染色体分配错误而分隔开。总的来说, 总共 285 个 RAD 标记中的 11 个标记并不能确保被分配到预期的染色体。连锁群 28 在单个位点仅包含 4 个 RAD 标记。从其余的未分配到连锁群的父本标记中, 用 JoinMap 3.0 识别出了 6 个额外标记。

Figure 2 Linkage map of the *Plutella xylostella* (n = 31) genome (Adopted from Baxter et al., 2011B)

Note: This was inferred from 2,878 RAD alleles collapsed into 285 discrete RAD markers. Each linkage group contains between 10 and 158 RAD alleles (labelled RADs) and the total map length is 1,292 cM. Each RAD marker is labelled with three numbers (i ii iii) corresponding to (i) the RAD marker (1-285), (ii) the chromosome number (1-31) and (iii) the number of RAD alleles at that marker. Linkage groups 1-28 are homologous to the *B. mori* (n = 28) chromosome numbering system, and LG29, LG30 and LG31 represent fusions to chromosomes 11, 23 and 24 respectively in *B. mori*. Dashed lines represent manual linkages inferred from 3, 4 or 5 genotype differences that were otherwise left ungrouped due to small sample size. As 20 progeny were used to construct the map, distances were approximated as 5 cM (1/20) per 1 crossing-over (c/o) event. On chromosomes 14, 16 and 22, markers formed two distinct groups and may be separated by regions of high recombination rates or chromosomal assignment error. In total, 11 of the 285 RAD markers could not be confidently assigned to their predicted chromosome. Linkage group 28 contained only four RAD markers at a single locus. Six additional markers were identified for this chromosome using JoinMap 3.0, from the remaining paternal markers not assigned to linkage groups





#### 4 小菜蛾的分子适应

小菜蛾通常认为起源于欧洲。1854 年首次在 Illinois 发现, 1883 年蔓延到 Florida 和 Rocky Mountains, 1905 年在 British Columbia 有报道, 如今在全球有白菜种植的每个角落都发现了这种昆虫(Furlong et al., 2012)。显然, DMB 适应了各种环境的挑战, 这种对外界环境的适应与小菜蛾在幼虫阶段偏好表达的基因, 发现与气味感受、食物消化和解毒代谢相关的基因所构成的复杂基因网络密切相关。

早在 1950 年代就报道了小菜蛾具有抗 DDT 的能力(Ankersmit et al., 1953); 1990 年代报道了小菜蛾抗 Bt 毒素的能力(Heckel et al., 1999, Tabashnik et al., 1999)。迄今, 小菜蛾几乎能对所有种类的农药产生抗性, 这要归功于小菜蛾在长期进化过程中形成生物解毒代谢途径, 使得小菜蛾拥有对很多化学物质具有解毒能力 (You et al., 2013), 从而使其成为一个臭名昭著的鳞翅目害虫。

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