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昆虫生理生化

Insect Physiology and Biochemistry

（双语教材）

(Bilingual Textbook)

主编　李文楚

Edited　by Li Wenchu

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内容简介

Brief Introduction

Insect Physiology and Biochemistry ia an important course of entomology subject. It developed very well recently. Educational circles of insectology get more and more contacts with overseas parties. Biligual education was proved to be an effective approach to culture students for opening their view points, adjusting the strucutre of professional knowledge, understanding frontier of the subject and acting on international convention.

昆虫生理生化是昆虫学科的一门重要课程，发展非常迅速。昆虫学界对外联系交往也越来越多；双语教学成为培养学生开拓视野，调整专业知识结构，了解学科发展前沿以及与国际接轨的重要途径。

The book is divided into 16 chapters. To promote innovation, it begin with brief history of researches in insect physiology, systematically introduce the structure and chemical components and process of integument, digestion and nutrition, fat body and intermediary metabolism,respiration system, hemolymph and circulatory system, insect hormones, excretion system, sensory system, light and visual sensory, neuroanatomy and neuropeptides, insect nerve system and physioloy, muscle and movement, pheromones, reproductive system and its biochemical process, insect diapause, and insect immunity. The contents is arranged by the sequence of organization structure of insect apparatus, physiological processes and biochemical reactions. They will be deployed from section to chapter with bilingual contrast. In additon to the essential speculative knowledge, it emphases the advanced researches and developmental trend of the subject.

本书共十六章。从昆虫生理学研究的简要历史发展入手，系统介绍昆虫体壁组成及其生化反应，消化与营养，脂肪体与中间代谢，呼吸系统，血淋巴循环系统，昆虫激素，排泄系统，昆虫感觉系统，光和昆虫视觉感受器，神经解剖与神经肽，昆虫神经生理生化，肌肉与运动，信息化合物，生殖及其生化学，昆虫滞育和昆虫免疫。内容上按各器官系统组织结构、生理进程和生化反应的过程逐章逐节展开，中英文对照。 除了基本的理论知识，重点介绍学科领域的最新进展和发展趋势。

The book will be suitable for bilingual education in domestic agricultural academy. Offering undergraduate and postgraduate entomological students, researchers and relative technologists, the textbook is an excellent references.

本书适用于国内高等农业院校开展昆虫生理生化双语教学，供昆虫学本科生、研究生、研究人员和昆虫学相关行业专业技术人员参考。

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绪 论

PREFACE

Insects (from Latin *insectum*) are a class of living creatures within the arthropods that have a chitinous exoskeleton, a three-part body (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and one pair of antennae. They are among the most diverse groups of animals on the planet, including more than a million described species and representing more than half of all known living organisms. The numbers of extant species is estimated at between six and ten million, and potentially represent over 90% of the differing metazoan life forms on Earth (Fig.1). So far, fossilized insects of enormous size have been found from the Paleozoic Era, including giant dragonflies with wingspans of 55 to 70 cm. Insects may be found in nearly all environments, although only a small number of species occur in the oceans, a habitat dominated by another arthropod group, crustaceans.

昆虫（来自拉丁语 *insectum*）是节肢动物门的一个纲，具有几丁质外壳，三部分躯体（头、胸、腹部），三对有关节的腿，复眼，一对触角。它们是这个星球上种群最多样化的动物，已描述的物种超过百万，代表着半数以上已知的生物有机体。现存物种的数量估计在600到1000万之间，可能代表着超过 90%的地球上不同的多细胞生活形式（图 1）。至今，发现古生代规模巨大的昆虫化石，如巨型蜻蜓，其翅展 55~70cm。昆虫几乎在所有环境中随处可见，但只有少部分在海洋中出现的物种，那里主要栖息着节肢动物的另一个种群，甲壳纲。

The life cycles of insects vary, but most hatch from eggs. Insect growth is constrained by the inelastic exoskeleton and development involves a series of molts. The immature stages can differ from the adults in structure, habit and habitat, and can include a passive pupal stage in those groups that undergo complete metamorphosis. Insects that undergo incomplete metamorphosis lack a pupal stage and adults develop through a series of nymphal stages.

昆虫的生活周期不同，但多数从卵孵化。昆虫的成长受到毫无弹性的外骨骼限制，因而发育牵涉到一连串的蜕皮。成虫结构、习性和栖息地从幼龄期即可不同，对那些进行完全变态的昆虫还包括一个静态的蛹期。不完全变态昆虫没有蛹期，成虫通过一系列若虫发育。

Insects typically move about by walking, flying or sometimes swimming. As it allows for rapid yet stable movement, many insects adopt a tripedal gait in which they walk with their legs touching the ground in alternating triangles. Insects are the only invertebrates to have evolved flight. Many insects spend at least part

昆虫通常靠行走、飞行或时而游泳到处活动。考虑到快速而稳定的运动，许多昆虫采用三足步法行走，其腿以交互三角接触地面。昆虫是通过进化飞行的唯一的无脊椎动物。许多昆虫至少在水下度过部分生涯，以幼虫适应，包括气门

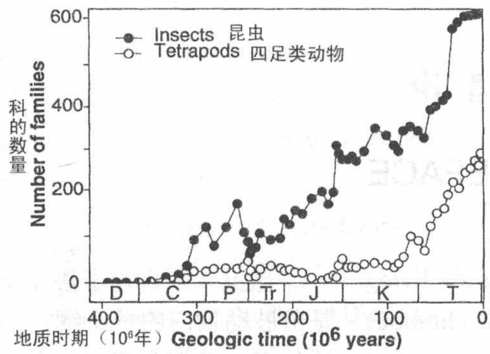

图 1 地质时期化石昆虫科的数量多样性（仿 Labanderia 等，1993）。缩写：D，泥盆纪；C，石炭纪；P，二叠纪；J，侏罗纪；K，白垩纪；T，第三纪。

Fig.1 Family-level diversity of fossil insects through geologic time (modified from Labanderia *et al.*, 1993). Abbreviation are D,Devonia; C,Carboniferous; P, Permian; J,Cretaceous; T, Tertiary.

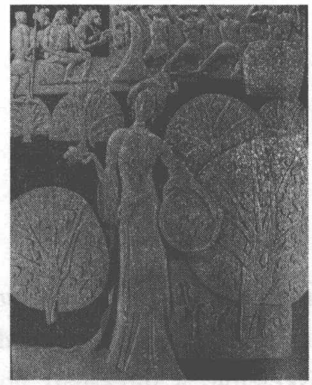

图 2 中国蚕神嫘祖，传说的皇后和黄帝的妻子。据说她发现了蚕丝，发明了丝织机。

Fig.2 Chinese silkworm God, Leizu, who was a legendary empress and wife of Huangdi. According to tradition, she discovered silk and invented the silk loom.

of their lives underwater, with larval adaptations that include gills, and some adult insects are aquatic and have adaptations for swimming. Some species, such as water striders, are capable of walking on the surface of water. Insects are mostly solitary, but some, such as certain bees, ants, and termites, are social and live in large, well-organized colonies. Some insects, such as earwigs, show maternal care, guarding their eggs and young. Insects can communicate with each other in a variety of ways. Male moths can sense the pheromones of female moths over great distances. Other species communicate with sounds: crickets stridulate, or rub their wings together, to attract a mate and repel other males. Lampyridae in the beetle order Coleoptera communicate with light.

According to the Chinese legend, the technology of raising silkworms was invented and created by Leizu (Fig.2), which indicates the long history of Chinese sericulture, in the middle of Neolithic Period, dating from 3000 B.C. It witnessed the rising of many variations of this insect in the voltinism, the molting character, markings, body size and shape of the larvae, and the color,

鳃，有些昆虫成虫是水生的，适应游泳。有些物种，如水黾，能在水面行走。多数昆虫为独居，但有些昆虫诸如蜜蜂、蚂蚁和白蚁是社会性的，生活在庞大而有组织性的群体内。有些昆虫（如蠼螋）呈现出母系呵护，对其卵和幼虫进行监护。昆虫通过各种途径相互联系。雄蛾能在很长距离感受雌蛾的信息素。其他种群通过声音联系：如蟋蟀的唧唧鸣叫，或用它们的翅膀相互摩擦来引诱交配，并抵制其他雄虫。甲壳鞘翅目的萤科昆虫用光线沟通。

根据中国传说，养蚕技术是嫘祖（图 2）发明创造的，象征着中国蚕桑的悠久历史追溯到新石器时期中期，公元前三千年。它见证了这一昆虫在化性、蜕皮特性、斑纹、幼虫体型和形状，以及茧色、茧形和丝质的许

shape and silk quality of the cocoons.

Insect parasitism was known in China for a long time in the form of parasitic tachinid flies of silkworms (*B. mori* L.). These tachinid flies were first mentioned in the Chinese literature around 300 AD. The developmental cycle of this tachinid (possibly a species of the genus Exorista) were clearly described in 1096. This antedates the first descriptions of insect parasitoids from Europe by 600 years. Another parasitic fly, a flesh fly (possibly *B. lapidosa* Pape) was noted as the main parasitoid of *L. migratoria* manilensis Meyen in 1196. In 1578, a famous Chinese medical book, "Compendium of Materia Medica" recorded a numbers of insects were used as Chinese Medicine，such as cordyceps sinensis and stiff silkworm. The first Chinese record with a correct description of the life cycle of a hymenopteran parasitoid dates from 1704 (Cai *et al*., 2005).

Ancient Sumer, the civilization near the river Euphrates, is the cradle of beekeeping, created about 3000-3500 BC. In ancient Egyptian poetry honey was used also as a symbol of love. In the few poems written between 1100 and 2000 BC and transmitted into our times. Archaeological finds relating to beekeeping have been discovered at Rehov, a Bronze and Iron Age archaeological site in the Jordan Valley, Israel.Thirty intact hives, made of straw and unbaked clay, were discovered in the ruins of the city, dating from about 900 BC. In ancient Greece, aspects of the lives of bees and beekeeping are discussed at length by Aristotle. The art of beekeeping appeared in ancient China for a long time and hardly traceable to its origin. In the book "Golden Rules of Business Success" written by Fan Li (or Tao Zhu Gong) during the Spring and Autumn Period there are some parts mentioning the art of beekeeping and the importance of the quality of the wooden box for beekeeping that can affect the quality of its honey.

It was not until the 18th century that European natural philosophers undertook the scientific study of bee colonies

多演化。

昆虫寄生虫在中国很久以前就广为人知，其形式是家蚕的寄生性蝇蛆。这些寄生蝇早在大约公元 300 年的中国文献中第一次被提及。1096 年，明确描述了寄生蝇的发育周期（可能是家蚕追寄蝇属的一个种），先于欧洲最早的昆虫寄生虫记录六百年。1196 年，另一种寄生麻蝇（可能是线纹折麻蝇）被记录为飞蝗的主要寄生虫。1578 年，中医药名著《本草纲目》记载，一些昆虫可作为中药，如冬虫夏草和僵蚕。1704 年，中国第一次记录了膜翅目寄生虫的准确的生活周期（Cai 等，2005）。

幼发拉底河畔的古苏美尔文明是养蜂业的发源地，创立于公元前 3000~3500 年。古埃及诗歌里，蜂蜜被当做爱情的符号，少数诗歌创作于公元前 1100~2000 年，并传承至我们的年代。拉霍夫是以色列约旦河谷青铜器和铁器时期遗址，其考古学发现与养蜂业有关。在公元前 900 年的城市遗址发现 30 个用麦秆和未熟粘土制成的完整蜂箱。古希腊，Aristotle 详尽地讨论了蜜蜂生活方式的各个方面及其养蜂业。古代中国的养蜂工艺出现在很久以前，几乎难以追踪其起源。春秋时期的范蠡（或陶朱公）所著《致富奇术》中有些地方提及养蜂，养蜂木箱质量的重要性在于能影响蜂蜜的质量。

直到十八世纪，欧洲的自然科学家才着手蜂群的科学研究，开始弄懂蜜蜂生物学复杂而神

and began to understand the complex and hidden world of bee biology. Preeminent among these scientific pioneers, Swammerdam and Réaumur were the first to use a microscope and dissection to understand the internal biology of honey bees. Réaumur observed queens laying eggs in open cells, but still had no idea of how a queen was fertilized; nobody had ever witnessed the mating of a queen and drone and many theories held that queens were "self-fertile," while others believed that a vapor or "miasma" emanating from the drones fertilized queens without direct physical contact. Huber was the first to prove by observation and experiment that queens are physically inseminated by drones outside the confines of hives, usually a great distance away. Huber confirmed that a hive consists of one queen who is the mother of all the female workers and male drones in the colony. Together, he and Burnens dissected bees under the microscope and were among the first to describe the ovaries and spermatheca, or sperm store, of queens as well as the penis of male drones. Huber is universally regarded as "the father of modern bee-science" and his "New Observations on Bees" revealed all the basic scientific truths for the biology and ecology of honeybees.

In 1906, Morgan (Fig.3) began his work on *D. melanogaster* and reported his first finding of a *white* (eyed) mutant in 1910 to the academic community. He was in search of a model organism to study genetic heredity and required a species that could randomly acquire genetic mutation that would visibly manifest as morphological changes in the adult animal. His work on *Drosophila* earned him the 1933 Nobel Prize in Medicine for identifying chromosomes as the vector of inheritance for genes. This and other *Drosophila* species are widely used in studies of genetics, embryogenesis, and other areas.

Malpighi, the founder of comparative physiology, Italian physician and biologist who, in developing experimental methods to study living things, founded the science of

秘的世界。这些科学先驱的佼佼者 Swammerdam 和 Réaumur，第一个应用显微镜和切片观察蜜蜂的内部器官生物学。Réaumur 观察到蜂王在开放的小室产卵，但对蜂王如何受精毫无头绪；没有人见到过蜂王和雄蜂交配，许多理论认为蜂王是“自体授精，”而其他人相信雄蜂射出水气或“雾气”使蜂王受精而无直接体接触。Huber 是第一个通过观察和实验证明蜂王是由雄蜂在蜂巢外区域，通常在很远的距离外生理受孕。Huber 证实，蜂群有一个蜂王，是蜂群所有雌工蜂和雄蜂的母蜂。他与 Burnes 一道在显微镜下解剖蜜蜂，是所有研究者中第一个描绘蜂王卵巢、受精囊或储精囊，以及雄蜂的阳茎。Huber 被尊称为“现代蜜蜂科学之父”，其“蜜蜂新观察”揭示了蜜蜂生理和生态学的所有基本科学真理。

1906 年，Morgan（图 3）着手果蝇的研究；1910 年向学术界报道了第一个白眼突变体的发现。他在寻找一种模式生物研究基因遗传性，需要一个能随机获得基因突变的物种，在成年动物表现出明显的形态变化。他在果蝇上的研究使他获得 1933 年的诺贝尔医学奖，以表彰他确认染色体是遗传物质基因的载体。这个品系和其他果蝇品系已被广泛应用于遗传学、胚胎发生学和其他领域。

意大利生理学家和生物学家 Malpighi 是比较生理学奠基人，发展了活体生物的研究方

microscopic anatomy. He conducted many studies of insect larvae, the most important of which was his investigation in 1669 of the structure and development of the silkworm. The Malpighian tubule system is a type of excretory and osmoregulatory system found in some Atelocerata (Insects and Myriapoda), arachnids and tardigrades. The system consists of branching tubules extending from the alimentary canal that absorbs solutes, water, and wastes from the surrounding hemolymph. The wastes then are released from the organism in the form of solid nitrogenous compounds. The system is named after Malpighi. In 1762, the French anatomist, Lyonet, described as “granulated vessels”, a pair of minute organs located within the thorax of caterpillars. This description was soon forgotten and for 187 years has been buried among the literature pertaining to insect anatomy. Meanwhile, within the twentieth century, the very same organs have been, and apparently continue to be, rediscovered by various investigators (William, 1949). These organs, now known as “prothoracic glands” are among the most important endocrine glands in insects.

法，创立了显微解剖科学。他创造了很多研究昆虫幼虫的方法，最重要的发现是 1669 年的家蚕结构和发育的研究。马氏管系统是在一些缺角类动物（昆虫纲和六足类）、蛛形纲动物和多足类动物发现的。该系统由分枝的细管组成，从消化道延伸以便吸收周围血淋巴中的溶质、水分和废料。废料最后从有机体以固态氮化合物形式排放。这个系统以马尔皮基名字命名。1762 年，法国解剖学家 Lyonet 描述了位于毛虫胸部的一对极小的器官“粒状小管”。他的描述很快被人遗忘，并一直被埋藏在昆虫解剖学相关的文献中达 187 年。其间的二十世纪，不同的学者陆续重新发现了非常相似的器官（William,1949）。现在已知这些器官就是“前胸腺”，昆虫最重要的内分泌腺体。

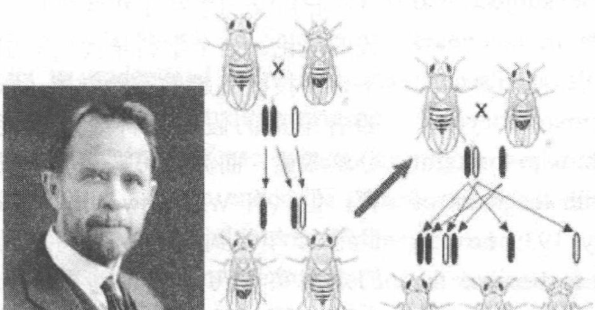

图 3 Morgan 和他的研究果蝇白眼突变体（网络综合图）。

Fig.3 Morgan and his work on *D. melanogaster white* (eyed) mutant(synthetic figure from internet).

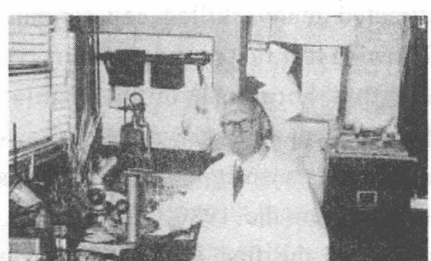

图 4 “昆虫生理学之父” Wigglesworth。

Fig.4 “The father of insect physiology” V. B. Wigglesworth(Edwards, 1998)

A thread that runs a tortuous course from Aristotle’s time through the 19th century, visualizing the insect larva and pupa as active embryos was broken by Darwin, who

从 Aristotle 年代到 19 世纪的线索曲折地行进，将昆虫幼虫和蛹当成活跃胚胎的设想被

saw the relationship of larva and pupa to the adult insect, with the pupa as a bridge passage. That concept of metamorphosis as sequential polymorphism finally crystallized out to a spare sentence: "Metamorphosis is merely one type of polymorphism" in V.B.Wigglesworth's (Fig.4) slim monograph "The Physiology of Insect Metamorphosis" (1954).

Weismann (1864), who first fully recognized the function and significance of the imaginal discs, illustrated 100 years earlier by Lyonet (1762), who proposed the "germplasm" theory of heredity. The germplasm theory states that an organism's cells are divided into somatic cells (the cells that make up the body) and germ cells (cells that produce the gametes). But the mechanisms of molting and postembryonic development remained mysterious even long after the importance of hormones had been recognized in the vertebrates. Kopéc's (1922) experiments, leading to the then heretical proposal that the insect brain secreted a hormone responsible for metamorphosis, opened the book to the final chapter in the endocrine physiology of postembryonic development of insects, and yet it was to take another thirty years before a coherent theory emerged. The subject had attracted many skilled experimentalists in the years following that first postulate that nerve cells could secrete and that hormones might regulate postembryonic development, but it was Wigglesworth who brought together his own brilliant experiments with the work of others, from the 1930's to the 50's. By 1939 he had completed the first edition of what was to become the bible of a new discipline: "The Principles of Insect Physiology". With *Rhodnius* he first showed by implantation experiments that protocerebral neurosecretory cells were the source of the hormone that initiates the molting cycle (Wigglesworth, 1939). This finding, building on Kopéc's, was the first experimental demonstration of an endocrine role for neural cells in any animal. But molting and growing are not the only processes to need explanation: what regulates maturation and metamorphosis in insects? The first indication that the assumption of adult

Darwin 打断，他考虑到了昆虫幼虫和蛹与成虫的关系，其间蛹起着桥梁通道作用。变态的概念就是时序化的多态性，最后凝炼成简化的命题：在 Wigglesworth（图4）单薄的专著“昆虫变态发育生理学”（1954）中“变态只不过是多态的一种类型。”

Weismann（1864）第一个完全认识到成虫芽的功能及其重要性，并提出遗传的“种质”学说，虽然早在 100 年前 Lyonet（1762）已图例说明。种质理论认为，生物细胞被分裂成体细胞（组成躯体的细胞）和生殖细胞（产生胚子的细胞）。但直至认识到脊椎动物激素的重要性之前，蜕皮和胚后期发育机制仍然保持着神秘。Kopéc（1922）的实验得出“离经叛道”的提议，昆虫脑分泌的激素是变态的原因，这打开了昆虫胚后发育学书籍关于内分泌生理学的最后篇章，此后又用了三十年才出现一致的理论。这个学科早前已吸引了许多技能高超的实验学家，跟随者早期的假定是神经细胞能分泌激素，而激素可调节胚后发育；但只有 Wigglesworth 在 20 世纪 30 年代到 50 年代才将自己的杰出实验与其他人的工作联系在一起。1939 年，他完成了成为新学科圣经的第一版：“昆虫生理学原理”。他第一次用长红猎蝽通过移植实验证明，前脑的神经分泌细胞是启动蜕皮周期的激素来源（Wigglesworth, 1939）。这一基于 Kopéc 的实验，是第一个实验证明在若干动物中神经细胞内分泌作用的。但蜕皮和成长并不是需要说明的唯