Форма № Н - 3.04

NATIONAL UNIVERSITY OF LIFE AND ENVEROMENTAL SCIENCES OF UKRAINE
Department Entomology named after prof. M. Dyadechko

"APPROVED"
Dean Plant protection , Biotechnology and Ecology
Kolomiyetc Yu.V.
«____»________________ 2022

Reviewed and approved
on meeting of department __________
Protocol № __10__ of "_12__" __05 - 2022
Head of Department
Likar Ya.O.-

WORKER EDUCATIONAL COMPLEX

"GENERAL ENTOMOLOGY"

Field of knowledge _

Direction of training 202 "Plant protection and Guarantine"

Spatiality

Specialization

Faculty Protection products, Biotechnology and Ecology

Developers: c. a. s., a. p. Kava L.P.

KYIV-2022

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WORKER EDUCATIONAL PROGRAM

"General entomology"

Field of knowledge _

Direction of training 202 "Plant protection and Guarantine"

Spatiality

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Faculty Protection products, Biotechnology and Ecology

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KYIV-2022

1. CHARACTERIZATION OF DISCIPLINE "General entomology"

Field of knowledge, direction of training, specialty, qualification level		
Branch of knowledge	20	Agricultural science and food
Specialty	202	Protection and Plant Quarantine
The degree of higher education		Bachelor
Credits ECTS		6
Number of modules		6
The total number of hours		216

Characteristics of discipline	
Kind	compulsory
Total amount of hours	<u>98</u>
Amount of credits, corresponding to ECTS	3
Modules	3
Type of control:	<u>test</u>

The form of the educational process and the types of classes, amount of hours

	Internal students	External students
Year of training	3	
Semester	5,6	
Lectures	45	
Practical, seminars		
Laboratory work		
Self-instruction under direction		
Individual tasks		
Amount of hours on a week for internal student Auditory self-instruction including course work (project)	83	
Evaluation	Passed Exam	

Course Objectives

Students will be able to…

- ➢ Explain the importance of insects
- ➢ Describe basic insect structure and function
- ➢ Describe the basic classification of economically important insects
- ➢ Explain how insects affect humans

Course Outcomes

At the end of the course, you should be able to…

- ➢ Explain which order an insect belongs to
- ➢ Describe something about an insect's structure and function
- ➢ Increase your insect appreciation and decrease your entomophobia (ento - insect, phobia - fear)
- ➢ Not instinctively want to smash a bug!

2. The program of the course

- Full term full-time (part-time) form of study;

- Short term agenda (correspondence) learning.

Names of modules and themes	Amounts of hours											
	Internal						External					
	Common amount	including					Common amount	including				
		Lect.	P.	Labor.	Self-work	Self-work under direction		Lect.	P.	Labor	Self-work	Self-work under direction
1	2	3	4	5	6	7	8	9	10	11	12	13
Module 1. Formation of virology as a science and structural property of viruses												
Theme 1. Introduction. Subject main objectives of the subject "Applications of biotechnology in agriculture"		2				10						
Theme 2. Biotechnology recycling and waste bioconversion APC		2				10						
Total for module 1.		**4**				**20**						
Module 2. Spread of viruses and its influence on plants												
Theme 3 Biotechnological production processes entomological and microbiological preparations for plant protection. Biological plant protection.		2				13						

Theme 4. Biotechnological processes for production of biologically active fertilizers and biological products for the restoration and rehabilitation of soil productivity		2				10						
Theme 5. Biotechnological processes forage and fodder additives		2				10						
Total for module 2.		6				33						
Module 3. Spread viruses in nature												
Theme 6. Biotechnology and structural characteristics of domestic and foreign bioengineering systems based on complex integrated vzayemouvyazanomu use ahrobiotehnolohiy		2				13						
Theme 7. Methodological bases of research, evaluation and drafting of complex use of biotechnological processes concerning the conditions of specific agricultural or agricultural landscapes		2				8						

Theme 8. Methodology of scientific, theoretical and experimental research on the development and implementation of applications ahrobiotehnolohiy		1				9						
Total for module 3.		5				30						
Common amount of hours		15				83						

3. THEMES OF SEMINAR

№	Theme	Amount of hours
1	It does not foreseen by plan	

4. THEMES OF HANDS-ON LEARNING

№	Theme	Amount of hours
1	It does not foreseen by plan	

5. SUBJECT OF LABORATORY WORKS

№	Theme	Amount of hours
1	Determination of secondary raw materials and the calculation of the possible biogas output on livestock farms and complexes	1
2	Biotechnological processes and devices for the production of microbiological preparations for plant protection. Methods for determining key indicators of process and quality of the mikrobiopreparatu	2
3	Identification of possible vermicompost production volumes and calculating the basic technological parameters vermyhospodarstva in a particular agricultural enterprise	2
4	Bioenergy assessment biotechnological processes	1
	Total amount	6

6. TEST QUESTION TEST KITS TO DETERMINE THE LEVEL OF LEARNING STUDENTS.

7.

1. **Question 1.** Write the main characteristic Oder Diplura.
2. **Question 2.** Write about characteristics non-insect hexapods (Protura, Diplura, Collembola)

Tests

1. After passing through a spiracle, air diffusing throughout a complex, branching network of:

A. tracheal trunk
B. tracheal tubes
C. taenidia
D. air sacs.

2. How much are basic components that form "mandibulate" mouthparts

A. five
B. four
C. three
D. six

3. How called organ that allows dissolved oxygen from the water to pass (by diffusion) into an organism's body. In insects, this organ are usually outgrowths of the tracheal system and are covered by a thin layer of cuticle that is permeable to both oxygen and carbon dioxide:

A. Biological Gills
B. Breathing Tubes
C. Air Bubbles
D. Plastrons
E. Hemogoblin

4. Which order from Apterygote insects have survived to the present time.

A. Archaeognatha,
B. Thysanura,
C. Monura.

5. How called the side of each segment, that is usually divided by a pleural suture into at least two sclerites:

A. pleuron

B. episternum

C. epimeron

6. Labium is subdivided into the following parts:

A. Postmentum and Prementum

B. Cardo, Stipes, Galea and Lacinia

7. How called the leg, adapted for running:

A. Cursorial

B. Raptorial

C. Fossorial

D. Saltatoria

8. The dorsal sclerite of of the abdomen called:

A. tergum

B. sternum

C. pleural membrane

9. How called the egg-laying mechanism of females:

A. ovipositor

B. valvifers

C. valvulae

D. aedeagus

10. Hemimetabola insects group have next developmental stages in the life cycle:

A. egg,

B. larva,

C. pupa,

D. adult (imago).

8. FORMS OF CONTROLS

Rating of student from mastering of discipline is determined for 100 a ball scale. It consists of rating from educational work, at the evaluation of which 70 marks target, and rating from attestation (to examination) are 30 marks. Every semantic module is also estimated for 100 a ball scale.

On the rating of educational work by decision of the department can influence rating of additional work to □ 20 points and ranking penalty (with negative sign) □ to 5 points.

Rating of student from educational work of R_{EW} is determined after a formula

$$\mathbf{R_{НР} = \frac{0,7\cdot(R^{(1)}_{M} + R^{(2)}_{M} + R^{(3)}_{M})}{3} + R_{ДР} - R_{ШТР},}$$

where R^1_{M}, R^2_{M}, R^3_{M} - rating estimation of 1th 2th and 3th modules on a 100 ball scale. R_{AW}, R_{PW} - accordingly rating from additional work and rating of penalty area.

Students, who have received 60 or more points from educational work, cannot take the examination, and obtain test scores "Automatically". In this case the rating of student from discipline (R_{DIS}) is equal to his rating of educational work.

$R_{DIS} = R_{EW}$

If a student wants to improve his ranking and improve the assessment of discipline, he must pass an exam. A exam is passed by students who has scored less than 60 points. For admission to exam a student must score at least 60 points from each module and in general - not less than 42 points from educational work.

Rating of student from attestation (R_{AT}) is determined on a 100-point scale.

Rating of student from discipline (R_{DIS})is calculated by the formula.

$\mathbf{R_{DIS} = R_{EW} + 0,3 \times R_{AT}}$

Distribution Points that receive students. Evaluation of the student is in accordance with the provisions of "On the examinations and tests NUSEU in Ukraine" dated 02/20/2015. The protocol number 6 from the table. 1

national assessment	**Assessment YEKTS**		**student rating**
Excellent	**A**	**Excellent -** excellent performance with few errors	**90 – 100**
Good	**B**	**VERY GOOD -** above average with some mistakes	**82 – 89**
	C	**GOOD -** generally correct work with a number of blunders	**74 – 81**

Satisfactorily	**D**	**Satisfactory -** not bad but many drawbacks	**64 – 73**
	E	**ENOUGH -** performance meets the minimum criteria	**60 – 63**
Unsatisfactorily	**FX**	**Unsatisfactory -** must work before get credit (positive evaluation)	**35 – 59**
	F	**Poor -** thorough and elaborate	**01 – 34**

To determine the ranking of the student (listener) from mastering the discipline $\mathbf{R_{дис}}$ (100 points) received rating from certification (30 points) added to the ranking student (listener) for Academic $\mathbf{R_{НР}}$ (70 points):$\mathbf{R_{дис} = R_{НР} + R_{AT}}$.

LECTURE 1

General entomology –introduction

1.Why we should study Insects

2. How insects rule the world

3.How to ID insects

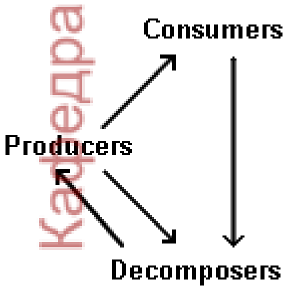
4. Summary

1.Why we should study Insects

We humans are such a self-centered species that we seldom stop to acknowledge or appreciate the importance of other living organisms in our environment. Our prowess in science and technology has given us unparalleled control over our physical environment, and as a result, we have developed an inflated view of our own importance in the web of life. Although we have learned to use tools, dam rivers, level mountains, and harness atomic power, we are still dependent on Mother Nature for the countless housekeeping chores that keep our environment stable and healthy. Indeed, we are relatively minor players in the ecological drama that continually unfolds all around us. If humans were to suddenly vanish from the planet, there would be no ecological calamity, no massive extinctions, and no tears shed for our demise. Remnants of human civilization would soon be smothered in vegetation, the forests would reclaim our cities, and life would go on without us just as it did for millions of years before our ancestors first reckoned the passage of time. Sadly, the earth would probably be better off without us.

2. How insects rule the world

In simplest terms, life (as we know it) exists on planet earth because of a global cycle of production and consumption that hinges almost exclusively on green plants as primary producers and insects as primary consumers. These two life-forms overshadow all other multi-cellular organisms in terms of abundance and diversity. They are mutually dependant on one another for survival, and form a nucleus around which all terrestrial and fresh-water ecosystems are built. Without green plants and the organic molecules they produce through photosynthesis, all animal life would collapse from starvation. Without insects and other decomposers, green plants would quickly exhaust their nutrient supplies, dead organic matter would accumulate in putrid, rotting heaps, and many species of flowering plants would become extinct for lack of insect pollinators.



In a sense, we owe our very existence to members of the insect world -- creatures we often fear or despise. We expend considerable resources trying to eliminate these animals from every facet of our daily lives, but in fact, we could never hope to survive without them -- they make the earth habitable for us. Like tiny maids and butlers, they perform Nature's housekeeping tasks with competence and efficiency. Nothing else -- animal, vegetable, or mineral -- could ever take their place. By virtue of their diversity, their world-wide distribution, their ecological importance, and their impact on other life-forms, the insects are indeed a class of distinction.

LECTURE 2

External Anatomy

1) A chitinous exoskeleton

2) Characteristics of exoskeleton

3) *Exoskeleton* provides

1. A chitinous exoskeleton

An insect's exoskeleton (integument) serves not only as a protective covering over the body, but also as a surface for muscle attachment, a water-tight barrier against desiccation, and a sensory interface with the environment. It is a multi-layered structure with four functional regions: epicuticle, procuticle, epidermis, and basement membrane.

1) Characteristics of exoskeleton

The epidermis is primarily a secretory tissue formed by a single layer of epithelial cells. It is responsible for producing at least part of the basement membrane as well as all of the overlying layers of cuticle. The basement membrane is a supportive bilayer of amorphous mucopolysaccharides (basal lamina) and collagen fibers (reticular layer). The membrane serves as a backing for the epidermal cells and effectively separates the hemocoel (insect's main body cavity) from the integument.

The procuticle lies immediately above the epidermis. It contains microfibers of **chitin** surrounded by a matrix of protein that varies in composition from insect to insect and even from place to place within the body of a single insect.

As the procuticle forms, it is laid down in thin lamellae with chitin microfibers oriented at a slightly different angle in each subsequent layer. In some parts of the body, procuticle stratifies into a hard, outer exocuticleand a soft, inner endocuticle.

Differentiation of exocuticle involves a chemical process (called **sclerotization**) that occurs shortly after each molt. During sclerotization, individual protein molecules are linked together by quinone compounds. These reactions "solidify" the protein matrix, creating rigid "plates" of exoskeleton known as **sclerites**. Quinone cross-linkages do not form in parts of the exoskeleton where resilin (an elastic protein) is present in high concentrations. These areas are **membranes** -- they remain soft and flexible because they never develop a well-differentiated exocuticle.

The epicuticle is the outermost part of the cuticle. Its function is to reduce water loss and block the invasion of foreign matter. The innermost layer of epicuticle is often called the cuticulin layer, a stratum composed of lipoproteins and chains of fatty acids embedded in a protein-polyphenol complex. An oriented monolayer ofwax molecules lies just above the cuticulin layer; it serves as the chief barrier to movement of water into or out of the insect's body. In many insects a cement layer covers the wax and protects it from abrasion.

In many insects, certain epidermal cells are specialized as exocrine glands. These large, secretory cells produce compounds (e.g. pheromones, repellants, etc.) that are released on the surface of the exoskeleton through microscopic ducts.

Tiny hair-like projections or surface sculpturing of the cuticle are known as microtrichae or pile (PILL-EE). These acellular structures consist of a solid core of exocuticle covered by a thin layer of epicuticle. Larger hairs, bristles, and scales (called setae or macrotrichae) are the product of two specialized epidermal cells: atrichogen cell (the hair shaft) and a tormogen cell (the socket). Multicellular projections of the exoskeleton are called spines (or spurs, if movable). They are lined with epidermis and contain both procuticle and epicuticle.

Skeletal muscles attach to the inner surface of the integument. Despite small body size, insects have many more muscles than vertebrates because the exoskeleton affords a larger surface area than an endoskeleton (relative to body volume) for muscle attachment. An insect owes its incredible strength to the geometry of its musculature -- providing optimal leverage for movement of appendages.

Invaginations (inward folds) of the exoskeleton add to its strength and rigidity. They also provide increased surface area for attachment of muscles. Ridge-like invaginations are called **apodemes**. They are usually visible externally as a groove (suture). Finger-like invaginations are called **apophyses**. A tiny pit usually marks their location externally.

The colors found in the integument of insects are produced either by pigment molecules, usually located in the cuticle, or by physical characteristics of the integument that cause scattering, interference, or diffraction of light. Pigments that are frequently present include the pterines, melanins, carotenoids, and mesobiliverdin. Color patterns may change over time. Rapid, temporary changes may occur in response to daily environmental conditions or to the threat of danger. Slower, more permanent changes are usually related to seasonal changes in the environment or hormonal influences.

LECTURE 3

The Insects head and antennae

1. The insects head

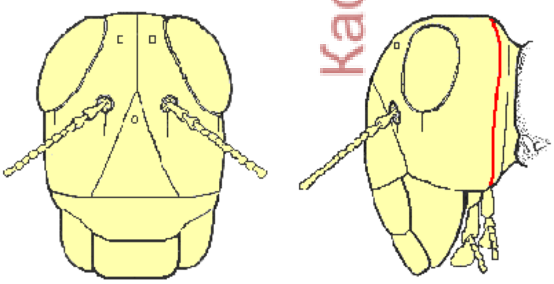
2. The insects antennae

1. The insects head

In most insects, the head capsule is a sturdy compartment that houses the brain, a mouth opening, mouthparts used for ingestion of food, and major sense organs (including antennae, compound eyes, and ocelli). Embryological evidence suggests that the first six body segments (three pre-oral and three post-oral) of a primitive worm-like ancestor may have fused to form the head capsule of most present-day insects.

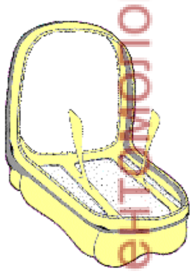
The surface of the head is divided into regions (sclerites) by a pattern of shallow grooves (sutures). The uppermost sclerite (dorsal surface) of the head capsule is known as the vertex. A coronal suture usually runs along the midline of the vertex and splits into two frontal sutures as it extends downward across the front of the head capsule. The triangular sclerite that lies between these frontal sutures is called the frons. The epistomal suture is a deep groove that separates the base of the frons from the clypeus, a rectangular sclerite on the lower front margin of the head capsule.

The genae ("cheeks") are lateral sclerites that lie behind the frontal sutures on each side of the head. Below each gena there may be another sclerite (the **subgena**), separated from the gena by a subgenal suture. A pair of compound eyes, sockets for two antennae, and one or more ocelli (simple eyes) also may be found on the front, top, or sides of an insect's head.



Near the back of the head, an occipital suture circumscribes the head capsule at the posterior margin of the vertex and genae. This suture marks the location of an internal sclerotized ridge (apodeme) that strengthens this part of the head capsule. Just behind the occipital suture lie the occiput and postgenae, tiny sclerites that are probably remnants of the fifth primitive segment that fused to form the insect's head. At the posterior-most margin of the head, a vestige of the sixth primitive segment is marked by a faintpostoccipital suture and a thin, band-like sclerite (the postocciput) that adjoins the neck membrane.

The insect's neck is known as the cervix. This is a membranous area that allows considerable freedom of movement for protraction and retraction of the insect's head.



Cut-away view of head capsule

The cervical membrane extends from the posterior portion of the postocciput to the prothorax, and it represents a transitional zone between the head and thorax. Small cervical sclerites serve as points of attachment for muscles that control head movements.

Inside the head, a structure called the tentorium serves as an internal "truss" that reinforces the head capsule, cradles the brain, and provides a rigid origin for muscles of the mandibles and other mouthparts. The tentorium forms during development when pairs of apophyses (finger-like invaginations of exoskeleton) fuse internally to create a "bridge". In most hemimetabolous insects, the tentorium is constructed from a pair of anterior arms and a pair of posterior arms(each "arm" represents a single apophysis). In some holometabolous insects, there are also a pair of dorsal arms that contribute to the structure. Externally, the location of each apophysis is often visible as a (anterior, posterior, or dorsal) "tentorial pit".

Antennae

The **antennae** are a pair of sense organs located near the front of an insect's head capsule. Although commonly called "feelers", the antennae are much more than just tactile receptors. They are usually covered with olfactory receptors that can detect odor molecules in the air (the sense of smell). Many insects also use their antennae as humidity sensors, to detect changes in the concentration of water vapor. Mosquitoes detect sounds with their antennae, and many flies use theirs to gauge air speed while they are in flight.

Although antennae vary widely in shape and function, all of them can be divided into three basic parts:

1. scape -- the basal segment that articulates with the head capsule
2. pedicel -- the second antennal segment
3. flagellum -- all the remaining "segments" (individually called **flagellomeres**)

2. The insects antennae

Types of Antennae:

The antennae of insects are modified in many ways. Some of these modifications just provide greater surface area for sensory receptors, while others are unique adaptations that bestow special sensory capabilities, such as detecting sound vibrations, wind speed, or humidity. The most common antennal types are listed below:

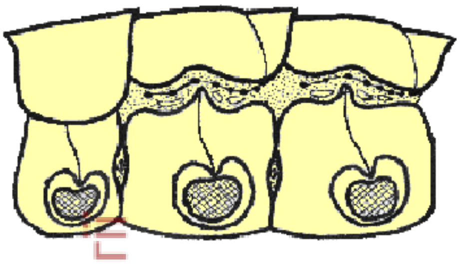
A. Filiform = thread-like
B. Moniliform = beaded
C. Serrate = sawtoothed
D. Setaceous = bristle-like
E. Lamellate = nested plates
F. Pectinate = comb-like
G. Plumose = long hairs
H. Clavate = gradually clubbed
I. Geniculate = elbowed
J. Aristate = pouch-like with one lateral bristle
K. Capitate = abruptly clubbed
L. All of these

LECTURE 4

Thorax

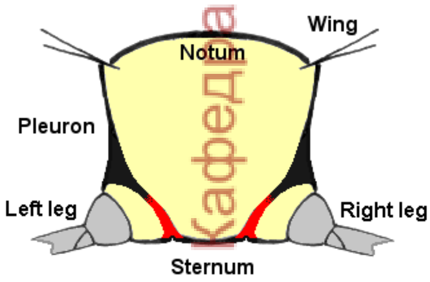
1. Thorax
2. Legs
3. Wings

1. Thorax



The second (middle) tagma of an insect's body is called the **thorax**. This region is almost exclusively adapted for locomotion -- it contains three pairs of walking legs and, in many adult insects, one or two pairs of wings.

Structurally, the thorax is composed of three body segments: prothorax, mesothorax, and metathorax. These segments are joined together rigidly to form a "box" that houses the musculature for the legs and wings. Each segment has a dorsal sclerite, the notum(pronotum, mesonotum, and metanotum) which may be further subdivided into an anterior **scutum** and a posterior **scutellum**. The ventral sclerite of each segment is the sternum (prosternum, mesosternum, and metasternum).The side of each segment is called the **pleuron** -- it is usually divided by a pleural suture into at least two sclerites:; an anterior episternum and a posterior epimeron.

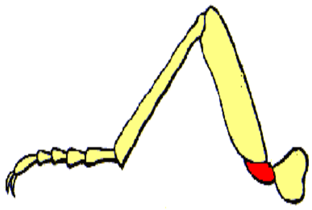


The pleural suture marks the location of an internal ridge of exoskeleton (an apodeme) that strengthens the sides of the thorax. Ventrally, this apodeme forms a point of articulation with the basal leg segment (the coxa). In thoracic segments that bear wings, the pleural apodeme runs dorsally into the pleural wing process, a finger-like sclerite that serves as a pivot or fulcrum for the base of the wing.

A special "strut" of exoskeleton reinforces the ventral corners of each thoracic segment and provides a rigid site for attachment of leg muscles and ventral longitudinal muscles.This structure, called the furca, forms during development when a pair of sternal apophyses fuse internally with the ridge (apodeme) from each pleural suture. The points of invagination are often visible externally as furcal pitslocated near the midline of the sternum (and often joined by a sternacostal suture). This internal "brace" mechanism is similar in structure to the tentorium which serves a related function inside the head capsule.

2. *Legs*

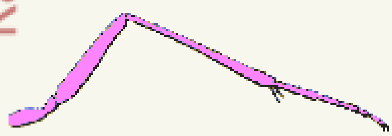
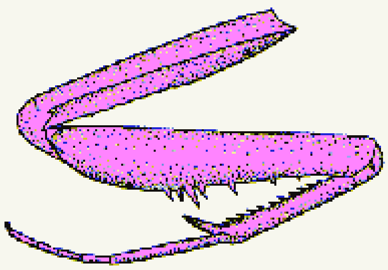
Most insects have three pairs of walking legs -- one pair on each thoracic segment. Each leg contains five structural components (segments) that articulate with one another by means of hinge joints:

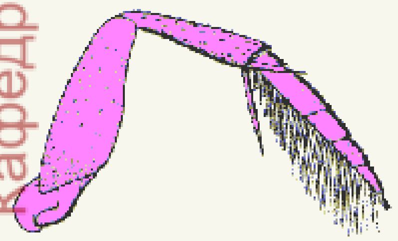
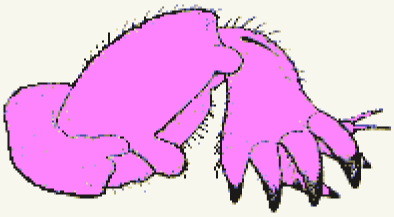
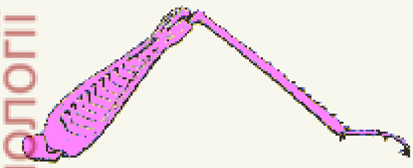


1. Coxa
2. Trochanter
3. Femur
4. Tibia
5. Tarsus

The term **pretarsus** refers to the terminal segment of the tarsus and any other structures attached to it, including:
ungues -- a pair of claws
arolium -- a lobe or adhesive pad between the claws
empodium -- a large bristle (or lobe) between the claws
pulvilli -- a pair of adhesive pads

Leg Adapations and Modifications:

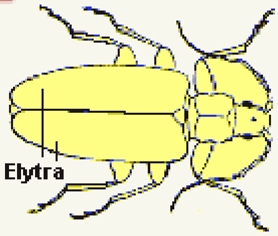
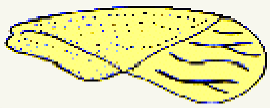
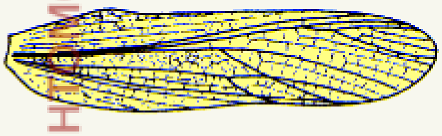
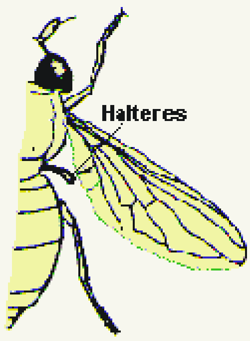
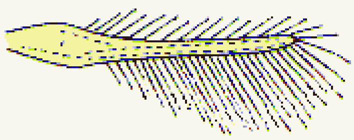
Characteristic	*Appearance*	*Example(s)*
Cursorial -- adapted for running		Ground beetles and Cockroaches
Raptorial -- adapted for catching and holding prey		Praying mantids

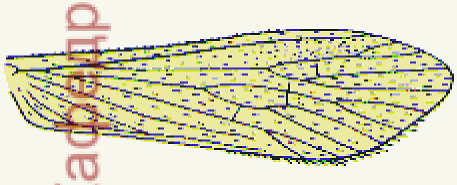
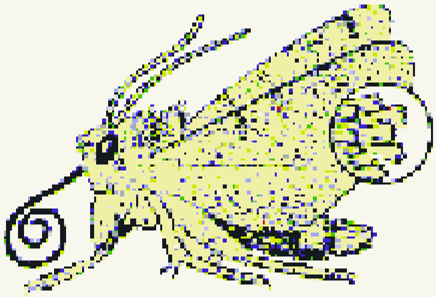
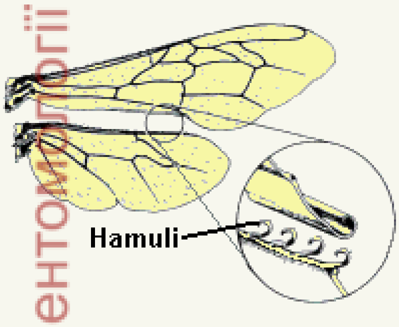
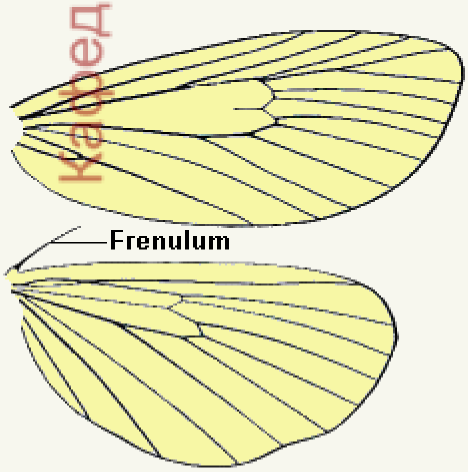
Natatorial -- adapted for swimming		Diving bugs and Water beetles
Fossorial -- adapted for digging in soil		Mole crickets
Saltatorial -- adapted for jumping		Grasshoppers

3.Wings

Insects are the only invertebrates that can fly. Their wings develop as evaginations of the exoskeleton during morphogenesis but they become fully functional only during the adult stage of an insect's life cycle. The wings may be membranous, parchment-like, heavily sclerotized, fringed with long hairs, or covered with scales. Most insects have two pairs of wings -- one pair on the mesothorax and one pair on the metathorax (never on the prothorax). Wings serve not only as organs of flight, but also may be adapted variously as protective covers (Coleoptera and Dermaptera), thermal collectors (Lepidoptera), gyroscopic stabilizers (Diptera), sound producers (Orthoptera), or visual cues for species recognition and sexual contact (Lepidoptera). In most cases, a characteristic network of veins runs throughout the wing tissue. These veins are extensions of the body's circulatory system. They are filled with hemolymph and contain a tracheal tube and a nerve. In membranous wings, the veins provide strength and reinforcement during flight. Wing shape, texture, and venation are quite distinctive among the insect taxa and therefore highly useful as aides for identification.

Wing adapations and modifications:

Characteristic	***Appearance***	***Order(s)***
Elytra -- hard, sclerotized front wings that serve as protective covers for membranous hind wings		Coleoptera and Dermaptera
Hemelytra -- front wings that are leathery or parchment-like at the base and membranous near the tip		Hemiptera: Heteroptera
Tegmina -- front wings that are completely leathery or parchment-like in texture		Orthoptera, Blattodea, and Mantodea
Halteres -- small, club-like hind wings that serve as gyroscopic stabilizers during flight		Diptera
Fringed wings -- slender front and hind wings with long fringes of hair		Thysanoptera

Hairy wings -- front and hind wings clothed with setae		Trichoptera
Scaly wings -- front and hind wings covered with flattened setae (scales)		Lepidoptera
Hamuli -- tiny hooks on hind wing that hold front and hind wings together		Hymenoptera
Frenulum -- Bristle near base of hind wing that holds front and hind wings together		Lepidoptera

Names of crossveins are based on their position relative to longitudinal veins:
c-sc crossveins run between the costa and subcosta
r crossveins run bewteen adjacent branches of the radius
r-m crossveins run between the radius and media
m-cu crossveins run between the media and cubitus

Locomotion

Insects are masters of movement: roaches run, bees swarm, moths fly, mantids strike, diving beetles swim, caterpillars crawl, dragonflies dart, maggots squirm, water boatmen paddle, mole crickets burrow, mosquito larvae wriggle, fleas jump, whirligigs spin, collembola spring, water striders skate, army ants march, and backswimmers dive. Indeed, the capacity for independent, goal-directed movement is one of the distinguishing characteristics that sets animals apart from most other forms of life on this planet.

Walking and Running

An exoskeleton can be awkward baggage, bulky and cumbersome for a small animal. To compensate, most insects have three pairs of legs positioned laterally in a wide stance. The body's center of mass is low and well within the perimeter of support for optimal stability. Each leg serves both as a strut to support the body's weight and as a lever to facilitate movement.

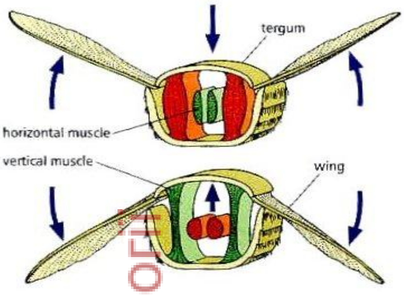
At very slow walking speeds an insect moves only one leg at a time, keeping the other five in contact with the ground. At intermediate speeds, two legs may be lifted simultaneously, but to maintain balance, at least one leg of each body segment always remains stationary. This results in a wave-like pattern of leg movements known as the metachronal gait. When running, an insect moves three legs simultaneously. This is the tripod gait, so called because the insect always has three legs in contact with the ground: front and hind legs on one side of the body and middle leg on the opposite side. Clearly, it is no coincidence that insects have exactly six legs -- the minimum needed for alternating tripods of support.

Coordination of leg movements is regulated by networks of neurons that can produce rhythmic output without needing any external timing signals. Such networks are called **central pattern generators** (CPGs). There is at least one CPG per leg. Individual networks are linked together via interneurons and output from each CPG is modified as needed by sensory feedback from the legs.

Only animals with a rigid body frame can use the tripod gait for movement. Soft-bodied insects, like caterpillars, have a hydrostatic skeleton. They move with peristaltic contractions of the body, pulling the hind prolegs forward to grab the substrate, and then pushing the front of the body forward segment by segment. This type of movement is exaggerated in larvae of Geometrid moths. While grasping the substrate with their six thoracic legs, they hunch the abdomen up toward the thorax, grasp the substrate with their prolegs, and then extend the anterior end as far as possible. This distinctive pattern of locomotion has earned them nicknames like "inchworms", "spanworms", and "measuringworms".

Flight

In all flying insects, the base of each wing is embedded in an elastic membrane that surrounds two (or three) axillary sclerites. One of these sclerites articulates with the pleural wing process, a finger-like sclerite that acts as a fulcrum or pivot point for the wing; a second sclerite articulates with the lateral margin of the mesonotum (or metanotum). Together, these elements form a complex hinge joint that gives the wing freedom to move up and down through an arc of more than 120 degrees. The hinge is a "bi-stable oscillator" -- in other words, it stops moving only when the wing is completely up or completely down. During flight, the wing literally "snaps" from one position to the other.



Power for the wing's upstroke is generated by contraction of **dorsal-ventral** muscles (also called tergosternal muscles). These are called "indirectflight muscles" because they have no direct contact with the wings. They stretch from the notum to the sternum. When they contract, they pull the notum downward relative to the fulcrum point and force the wing tips up. Elasticity of the thoracic sclerites and hinge mechanism allows as much as 85% of the energy involved in the upstroke to be stored as potential energy and released during the downstroke.

In the more primitive insect orders (*e.g.* Odonata and Blattodea), the downstroke is initiated by basalar muscles that attach through ligaments directly to the wing's axillary sclerites. Contraction of these "direct flight muscles" literally pulls the wings into their "down" position. Most other insects have **dorsal-longitudinal** muscles attached like bow strings to apodemes at the front and back of each thoracic segment. These are "indirectflight muscles". When they contract, they cause the edges of the notum to flex upward (relative to the fulcrum point) causing the wings to snap down.

During flight, upstroke and downstroke muscles must contract in alternating sequence. There are two different mechanisms for controlling this muscle action, synchronous (neurogenic) and asynchronous (myogenic):

Insects with **synchronous** control have **neurogenic** flight muscles, meaning that each contraction is triggered by a separate nerve impulse. Central pattern generators in the thoracic ganglia coordinate the rate and timing of these contractions. Since nerve cells have a refractory period that limits how often they can fire, insects with neurogenic flight muscles have relatively slow wing beat frequencies (typically 10-50 beats per second).

Insects with **asynchronous** control depend almost entirely on indirect flight muscles for upstroke (dorsal-ventrals) and downstroke (dorsal-longitudinals). These muscles have developed **myogenic** properties, that is, they contract spontaneously if stretched beyond a certain threshhold. When the nervous system sends a "start" signal, the dorsal-longitudinal and dorsal-ventral muscles begin contracting autonomously, each in response to stretching by the other. Contractions continue until the muscles receive a "stop" signal from the nervous system. Asynchronous control is not limited by the nerves' refractory period, so wing beat frequency in some of these insects (notably flies and bees) may be as high as 500-1000 beats per second. Such high frequencies produce greater lift with smaller surface area and also improve maneuverability (*e.g.* hovering, flying backwards, and landing upside down on the ceiling!)

As an insect's wing moves up and down during flight, it also twists about the vertical axis so that its tip follows an ellipse or a figure eight. This sculling motion maximizes lift on the downstroke and minimizes drag on the upstroke. Turning, hovering, and other acrobatic maneuvers are controlled by small muscles attached to the axillary sclerites. These muscles adjust the tilt and twist of the wing in response to feedback from the central nervous system and sensory receptors that monitor lift and thrust.

Swimming and Skating

Many aquatic beetles (Coleoptera) and bugs (Hemiptera) use their middle and/or hind legs as oars for swimming or diving. These legs are usually flattened or equipped with a fringe of long, stiff hairs to improve their performance and efficiency in the water. Legless larvae and pupae of mosquitoes, midges, and other flies (Diptera) manage to swim by twisting, contorting, or undulating their bodies. Dragonfly naiads (Odonata) have a jet propulsion system: they can propel themselves forward by contracting abdominal muscles and forcing a jet of water out of the rectal chamber that houses their respiratory gills.

A few aquatic insects, such as water striders, have a whorl of hydrophobic hairs on the tips of their feet. These hairs prevent the insect's legs from breaking the surface tension of the water and allow them to skate on the surface.

LECTURE 5

The Mouthparts

1. Basic components that form mouthparts
2. Modified Mandibulate Mouthparts
3. Haustellate Mouthparts

1. Basic components that form mouthparts

The ancestors of present-day insects were probably worm-like arthropods with a simple mouth opening near the front of a bilaterally symmetrical body. Over many eons of time, tissues and appendages near the mouth opening came to be adapted for gathering and manipulating bits of solid food. As insects evolved, they became more complex, expanded in range, and adapted to new food resources. The structure and function of their mouthparts changed right along with their evolving diet and life style. This is an excellent example of adaptive radiation (an evolutionary process in which two or more populations, exposed to different selective pressures, diverge from a common ancestor). Examples of adaptive radiation can be found just about everywhere in the insect world (think about variability in legs, wings, and antennae, for example). Entomologists pay close attention to mouthparts because their structure allows us to infer what type of food is consumed — plant or animal, solid or liquid, dead or alive. (Remember, **"Form Follows Function"** in biology). Knowing something about an insect's diet leads us to even more information about it's ecology and natural history.

Mandibulate Mouthparts

In all "primitive" insects, the mouthparts are adapted for grinding, chewing, pinching, or crushing bits of solid food. These are known as **"mandibulate"** mouthparts because they feature prominent chewing mandibles. There are five basic components that form these mouthparts:

1. Labrum — a simple plate-like sclerite that serves as a front lip to help contain the food.
2. Mandibles — a pair of jaws for crushing or grinding the food. They operate from side to side, not up and down.
3. Maxillae — paired appendages with the following parts:
    - **Cardo** — basal sclerite that articulates with the head capsule
    - **Stipes** — medial sclerite that supports a sensory **palp**

- **Galea** and **Lacinia** — distal sclerites that act as fork and spoon to manipulate the food

4. Hypopharynx — a tongue-like process that helps mix food and saliva.
5. Labium — a back lip that is derived from a pair of appendages that have fused together along the midline. It is subdivided into the following parts:
   - **Postmentum** — fused basal sclerites that articulate with the head
   - **Prementum** — distal sclerites that support another pair of sensory **palps** and divide apically to form four lobes; the two innermost lobes are called **glossae** and the two outermost lobes are called **paraglossae**.

Examples of insects with basic mandibulate mouthparts include grasshoppers, cockroaches, and ground beetles. Immature stages of many holometabolous insects (like beetle larvae and lepidopteran caterpillars) also have mandibulate mouthparts.

2. Modified Mandibulate Mouthparts

As insects evolved to feed on a wider variety of food resources, their mouthparts adapted accordingly through natural selection. In some cases, an individual component of the mouthparts became specialized for a new function. In weevils, for example, the front of the head is elongated into a long, slender proboscis. The mandibulate mouthparts are reduced in size allowing the insect to excavate a deep narrow hole that is used for feeding, and perhaps later, as a site for oviposition. In dragonfly naiads (immatures), the labium has become adapted as a prehensile tool that can be rapidly extended forward to catch prey.

3.Haustellate Mouthparts

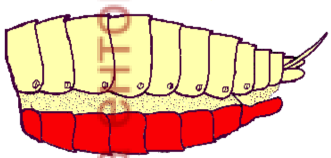
Some of today's more "advanced" insects have mouthparts that have become adapted for ingesting liquid food. These are collectively known as "haustellate" mouthparts (derived from the Latin verb "haustor" meaning to draw up or suck). They function in various ways: probing/sipping, sponging/lapping, piercing/sucking, etc. But regardless of how they work, they are still constructed from the same five building blocks found in mandibulate mouthparts: labrum, mandibles, maxillae, hypopharynx, and labium. Through natural selection and adaptive radiation, these parts have sometimes undergone radical changes in shape and function but they still occupy similar positions relative to each other (i.e. the labrum is always in the front and the labium is always in the back). Examples of insects with haustellate mouthparts include true bugs, aphids (and their relatives), butterflies and moths, fleas, mosquitoes and many other types of flies.

LECTURE 6
The Abdomen

1. The structure of abdomen
2. Abdominal structures
3. The insect's genital opening
4. Other abdominal structures

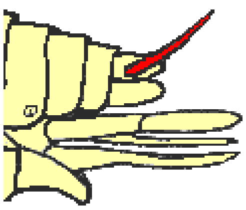
An insect's abdomen is the third functional region (tagma) of its body; the abdomen is located just behind the thorax. In most insects, the junction between thorax and abdomen is broad, but in some groups, the junction is very narrow (petiolate) giving the appearance of a "wasp-waist".

Entomologists generally agree that insects arose from primitive arthopod ancestors with eleven-segmented abdomens. Some present-day insects (e.g. silverfish and mayflies) still have all of these segments (or remnants of them), but natural selection in more advanced (or specialized) groups has contributed to a reduction in the number of segments -- sometimes to as few as six or seven (e.g. beetles and flies).



Each segment of the abdomen consists of a dorsal sclerite, the tergum, and a ventral sclerite, the sternum, joined to one another laterally by a pleural membrane. The front margins of each segment often "telecope" inside the sclerites of the preceding sement, allowing the abdomen to expand and contract in response to the actions of skeletal muscles.

At the very back of the abdomen, the **anus** (rear opening of the **digestive system**) is nestled between three protective sclerites: a dorsal epiproct and a pair of lateral paraprocts. A pair of sensory organs, the cerci, may be located near the anterior margin of the paraprocts. These structures are tactile (touch) receptors. They are usually regarded as a "primitive" trait because they are absent in the hemipteroid and holometabolous orders.



FEMALE

MALE

The insect's **genital opening** lies just below the anus: it is surrounded by specialized sclerites that form the **external genitalia**. In **females**, paired appendages of the eighth and ninth abdominal segment fit together to form an egg-laying mechanism called the ovipositor. These appendages consist of four valvifers (basal sclerites with muscle attachments) and six valvulae (apical sclerites which guide the egg as it emerges from the female's body). In **males**, the genital opening is usually enclosed in a tube-like **aedeagus** which enters the female's body during copulation (like a penis). The external genitalia may also include other sclerites (e.g. subgenital plate, claspers, styli, etc.) that facilitate mating or egg-laying. The structure of these genital sclerites differs from species to species to the extent that it usually prevents inter-species hybridization and also serves as a valuable identification tool for insect taxonomists.

Other abdominal structures may also be present in some insects. These include:

- **Pincers** -- In Dermaptera (earwigs), the cerci are heavily sclerotized and forceps-like. They are used mostly for defense, but also during courtship, and sometimes to help in folding the wings.
- **Median caudal filament** -- a thread-like projection arising from the center of the last abdominal segment (between the cerci). This structure is found only in "primitive" orders (e.g. Diplura, Thysanura, Ephemeroptera).
- **Cornicles** -- paired secretory structures located dorsally on the abdomen of aphids. The cornicles produce substances that repel predators or elicit care-giving behavior by symbiotic ants.
- **Abdominal prolegs** -- fleshy, locomotory appendages found only in the larvae of certain orders (notably Lepidoptera, but also Mecoptera and some Hymenoptera).
- **Sting** -- a modified ovipositor, found only in the females of **aculeate** Hymenoptera (ants, bees, and predatory wasps).
- **Abdominal gills** -- respiratory organs found in the nymphs (naiads) of certain aquatic insects. In Ephemeroptera (mayflies), paired gills are located along the sides of each abdominal segment; in Odonata (damselflies), the gills are attached to the end of the abdomen.
- **Furcula** -- the "springtail" jumping organ found in Collembola on the ventral side of the fifth abdominal segment. A clasp (the **tenaculum**) on the third abdominal segment holds the springtail in its "cocked" position.
- **Collophore** -- a fleshy, peg-like structure found in Collembola on the ventral side of the first abdominal segment. It appears to maintain homeostasis by regulating absorption of water from the environment.

LECTURE 7

Respiratory system

1. Structure of respiratory system

2. Respiration in aquatic insects

1. Structure of respiratory system

All insects are aerobic organisms -- they must obtain oxygen (O_2) from their environment in order to survive. They use the same metabolic reactions as other animals (glycolysis, Kreb's cycle, and the electron transport system) to convert nutrients (e.g. sugars) into the chemical bond energy of ATP. During the final step of this process, oxygen atoms react with hydrogen ions to produce water, releasing energy that is captured in a phosphate bond of ATP.

The respiratory system is responsible for delivering sufficient oxygen to all cells of the body and for removing carbon dioxide (CO_2) that is produced as a waste product of cellular respiration. The respiratory system of insects (and many other arthropods) is separate from the circulatory system. It is a complex network of tubes (called a **tracheal system**) that delivers oxygen-containing air to every cell of the body.

Air enters the insect's body through valve-like openings in the exoskeleton. These openings (called spiracles) are located laterally along the thorax and abdomen of most insects -- usually one pair of spiracles per body segment. Air flow is regulated by small muscles that operate one or two flap-like valves within each spiracle -- contracting to close the spiracle, or relaxing to open it.

After passing through a spiracle, air enters a longitudinal tracheal trunk, eventually diffusing throughout a complex, branching network of tracheal tubes that subdivides into smaller and smaller diameters and reaches every part of the body. At the end of each tracheal branch, a special cell (the **tracheole**) provides a thin, moist interface for the exchange of gasses between atmospheric air and a living cell. Oxygen in the tracheal tube first dissolves in the liquid of the tracheole and then diffuses into the cytoplasm of an adjacent cell. At the same time, carbon dioxide, produced as a waste product of cellular respiration, diffuses out of the cell and, eventually, out of the body through the tracheal system.

Each tracheal tube develops as an invagination of the ectoderm during embryonic development. To prevent its collapse under pressure, a thin, reinforcing "wire" of cuticle (the taenidia) winds spirally through the membranous wall. This design (similar in structure to a heater hose on an automobile or an exhaust duct on a clothes dryer) gives tracheal tubes the ability to flex and stretch without developing kinks that might restrict air flow.

The absence of taenidia in certain parts of the tracheal system allows the formation of collapsible air sacs, balloon-like structures that may store a reserve of air. In dry terrestrial environments, this temporary air supply allows an insect to conserve water by closing its spiracles during periods of high evaporative stress. Aquatic insects consume the stored air while under water or use it to regulate buoyancy. During a molt, air sacs fill and enlarge as the insect breaks free of the old exoskeleton and expands a new one. Between molts, the air sacs provide room for new growth -- shrinking in volume as they are compressed by expansion of internal organs.

Small insects rely almost exclusively on passive diffusion and physical activity for the movement of gasses within the tracheal system. However, larger insects may require active **ventilation** of the tracheal system (especially when active or under heat stress). They accomplish this by opening some spiracles and closing others while using abdominal muscles to alternately expand and contract body volume. Although these pulsating movements flush air from one end of the body to the other through the longitudinal tracheal trunks, diffusion is still important for distributing oxygen to individual cells through the network of smaller tracheal tubes. In fact, the rate of gas diffusion is regarded as one of the main limiting factors (along with weight of the exoskeleton) that prevents real insects from growing as large as the ones we see in horror movies!

2. RESPIRATION IN AQUATIC INSECTS

Aquatic insects need oxygen too! They are equipped with a variety of adaptations that allow them to carry a supply of oxygen with them under water or to acquire it directly from their environment. Read each of the following sections to learn about these adaptations and how insects use them to obtain oxygen and maintain an aquatic lifestyle.

Cuticular Respiration

Many aquatic species have a relatively thin integument that is permeable to oxygen (and carbon dioxide). Diffusion of gasses through this body wall (cuticular respiration) may be sufficient to meet the metabolic demands of small, inactive insects -- especially those living in cold, fast-moving streams where there is plenty of dissolved oxygen. Larger insects, more active ones, or those living in less oxygenated water may need to rely on other adaptations (see below) to supplement cuticular respiration.

Biological Gills

A **biological gill** is an organ that allows dissolved oxygen from the water to pass (by diffusion) into an organism's body. In insects, gills are usually outgrowths of the tracheal system. They are covered by a thin layer of cuticle that is permeable to both oxygen and carbon dioxide.

In mayflies and damselflies, the gills are leaf-like in shape and located on the sides or rear of the abdomen. Fanning movements of the gills keep them in contact with a constant supply of fresh water. Stoneflies and caddisflies have filamentous gills on the thorax or abdomen. Dragonflies differ from other aquatic insects by having internal gills associated with the rectum. Water is circulated in and out of the anus by muscular contractions of the abdomen. This rectal gill mechanism doubles as a jet propulsion system. A sudden, powerful contraction of the abdomen will expel a jet of water and thrust the insect forward -- a quick way to escape from predators.

Breathing Tubes

Although many aquatic insects live underwater, they get air straight from the surface through hollow breathing tubes (sometimes called **siphons**) that work on the same principle as a diver's snorkel. In mosquito larvae, for example, the siphon tube is an extension of the posterior spiracles. An opening at the end of the siphon is guarded by a ring of closely spaced hairs with a waterproof coating. At the air-water interface, these hairs break the surface tension of the water and maintain an open airway. When the insect dives, water pressure pushes the hairs close together so they seal off the opening and keep water out. Water scorpions (Hemiptera: Nepidae) and rat-tailed maggots (larvae of a syrphid fly) are two more examples of aquatic insects that have snorkel-like breathing tubes.

Many aquatic plants maintain their bouyancy by storing oxygen (a waste product of photosynthesis) in special vacuoles. A few insects (*e.g.* larvae of *Mansonia* spp. mosquitoes) insert their breathing tubes into these air stores and obtain a rich supply of oxygen without ever swimming to the surface of the water.

Air Bubbles

Some aquatic insects (diving beetles, for example) carry a bubble of air with them whenever they dive beneath the water surface. This bubble may be held under the elytra (wing covers) or it may be trapped against the body by specialized hairs. The bubble usually covers one or more spiracles so the insect can "breathe" air from the bubble while submerged.

An air bubble provides an insect with only a short-term supply of oxygen, but thanks to its unique physical properties, a bubble will also "collect" some of the oxygen molecules dissolved in the surrounding water. In effect, the bubble acts as a "physical gill" -- replenishing its supply of oxygen through the physics of passive diffusion. The larger the surface area of the bubble, the more efficiently this system works. An insect can remain under water as long as the volume of oxygen diffusing into the bubble is greater than or equal to the volume of oxygen consumed by the insect. Unfortunately, the size of the bubble shrinks over time as nitrogen slowly diffuses out into the water. When the bubble's surface area decreases, its rate of gas exchange also decreases. Eventually, the bubble becomes too small to keep up with metabolic demands and the insect must renew the entire bubble by returning to the water's surface.

Plastrons

A **plastron** is a special array of rigid, closely-spaced hydrophobic hairs (setae) that create an "airspace" next to the body. Air trapped within a plastron operates as a physical gill (just like air in a bubble) but this airspace cannot shrink in volume because the fortress of setae prevents encroachment of surrounding water. When the insect consumes oxygen, it creates a partial pressure deficit inside the plastron. This deficit is "corrected" by dissolved oxygen that diffuses in from the water. As nitrogen gradually diffuses out of the bubble, it creates a similar partial pressure deficit. But there is very little dissolved nitrogen present in water (it has a lower solubility potential than oxygen), so some of the nitrogen's partial pressure deficit is "corrected" by oxygen. In effect, the plastron "trades" some of the nitrogen for oxygen -- keeping a constant volume of gas that may slowly become "enriched" with oxygen.

The constant volume of a plastron's air supply eliminates the periodic need to surface and replenish the bubble. Insects that remain permanently submerged (ex. riffle beetles, family Elmidae) or lack the ability to reach the surface (ex. eggs of floodwater mosquitoes) are likely to have plastrons. These structures are often visible underwater as thin, silvery films of air covering parts of the body surface.

Hemogoblin

Hemoglobin is a respiratory pigment that facilitates the capture of oxygen molecules. It is an essential component of all human red blood cells, but it occurs only rarely in insects -- most notably in the larvae of certain midges (family Chironomidae) known as bloodworms. These distinctive red "worms" usually live in the muddy depths of ponds or streams where dissolved oxygen may be in short supply. Under normal (aerobic) conditions, hemoglobin molecules in the blood bind and hold a reserve supply of oxygen. Whenever conditions become anaerobic, the oxygen is slowly released by the hemoglobin for use by the cells and tissues of the body. This back-up supply may only last a few minutes, but it's usually long enough for the insect to move into more oxygenated water

LECTURE 8

The Digestive and Excretory Systems

1. Stomodeum
2. Mesenteron
3. Proctodeum

All insects have a complete digestive system. This means that food processing occurs within a tube-like enclosure, the alimentary canal, running lengthwise through the body from mouth to anus. Ingested food usually travels in only one direction. This arrangement differs from an incomplete digestive system (found in certain lower invertebrates like hydra and flatworms) where a single opening to a pouch-like cavity serves as both mouth and anus.

Most biologists regard a complete digestive system as an evolutionary improvement over an incomplete digestive system because it permits functional specialization-- different parts of the system may be specially adapted for various functions of food digestion, nutrient absorption, and waste excretion.

Proctodaeum

The pyloric valve serves as a point of origin for dozens to hundreds of Malpighian tubules. These long, spaghetti-like structures extend throughout most of the abdominal cavity where they serve as excretory organs, removing nitrogenous wastes (principally ammonium ions, NH_4^+) from the hemolymph. The toxic NH_4^+ is quickly converted to urea and then to uric acid by a series of chemical reactions within the Malpighian tubules. The uric acid, a semi-solid, accumulates inside each tubule and is eventually emptied into the hindgut for elimination as part of the fecal pellet.

The rest of the hindgut plays a major role in homeostasis by regulating the absorption of water and salts from waste products in the alimentary canal. In some insects, the hindgut is visibly subdivided into an ileum, a colon, and a rectum. Efficient recovery of water is facilitated by six rectal pads that are embedded in the walls of the rectum. These organs remove more than 90% of the water from a fecal pellet before it passes out of the body through the anus.

Embryonically, the hindgut develops as an invagination of the body wall (from ectodermal tissue). Just like the foregut, it is lined with a thin, protective layer of cuticle (intima) that is secreted by the endothelial cells of the gut wall. When an insect molts, it sheds and replaces the intima in both the foregut and the hindgut.

LECTURE 9

CIRCULATORY SYSTEM

Insects, like all other arthropods, have an **open circulatory system** which differs in both structure and function from the **closed circulatory system** found in humans and other vertebrates. In a closed system, blood is always contained within vessels (arteries, veins, capillaries, or the heart itself). In an open system, blood (usually called **hemolymph**) spends much of its time flowing freely within body cavities where it makes direct contact with all internal tissues and organs.

The circulatory system is responsible for movement of nutrients, salts, hormones, and metabolic wastes throughout the insect's body. In addition, it plays several critical roles in defense: it seals off wounds through a clotting reaction, it encapsulates and destroys internal parasites or other invaders, and in some species, it produces (or sequesters) distasteful compounds that provide a degree of protection against predators. The hydraulic (liquid) properties of blood are important as well. Hydrostatic pressure generated internally by muscle contraction is used to facilitate hatching, molting, expansion of body and wings after molting, physical movements (especially in soft-bodied larvae), reproduction (e.g. insemination and oviposition), and evagination of certain types of exocrine glands. In some insects, the blood aids in thermoregulation: it can help cool the body by conducting excess heat away from active flight muscles or it can warm the body by collecting and circulating heat absorbed while basking in the sun.

A dorsal vessel is the major structural component of an insect's circulatory system. This tube runs longitudinally through the thorax and abdomen, along the inside of the dorsal body wall. In most insects, it is a fragile, membranous structure that collects hemolymph in the abdomen and conducts it forward to the head.

In the abdomen, the dorsal vessel is called the heart. It is divided segmentally into chambers that are separated by valves (ostia) to ensure one-way flow of hemolymph. A pair of **alary muscles** are attached laterally to the walls of each chamber. Peristaltic contractions of the these muscles force the hemolymph forward from chamber to chamber. During each diastolic phase (relaxation), the ostia open to allow inflow of hemolymph from the body cavity. The heart's contraction rate varies considerably from species to species -- typically in the range of 30 to 200 beats per minute. The rate tends to fall as ambient temperature drops and rise as temperature (or the insect's level of activity) increases.

In front of the heart, the dorsal vessel lacks valves or musculature. It is a simple tube (called the aorta) which continues forward to the head and empties near the brain. Hemolymph bathes the organs and muscles of the head as it emerges from the aorta, and then haphazardly percolates back over the alimentary canal and through the body until it reaches the abdomen and re-enters the heart.

To facilitate circulation of hemolymph, the body cavity is divided into three compartments (called blood sinuses) by two thin sheets of muscle and/or membrane known as the dorsal and ventral diaphragms. The dorsal diaphragm is formed by alary muscles of the heart and related structures; it separates the pericardial sinus from the perivisceral sinus. The ventral diaphragm usually covers the nerve cord; it separates the perivisceral sinus from the perineural sinus.

In some insects, **pulsatile organs** are located near the base of the wings or legs. These muscular "pumps" do not usually contract on a regular basis, but they act in conjunction with certain body movements to force hemolymph out into the extremities.

About 90% of insect hemolymph is **plasma**: a watery fluid -- usually clear, but sometimes greenish or yellowish in color. Compared to vertebrate blood, it contains relatively high concentrations of amino acids, proteins, sugars, and inorganic ions. Overwintering insects often sequester enough ribulose, trehalose, or glycerol in the plasma to prevent it from freezing during the coldest winters. The remaining 10% of hemolymph volume is made up of various cell types (collectively known as **hemocytes**); they are involved in the clotting reaction, phagocytosis, and/or encapsulation of foreign bodies. The density of insect hemocytes can fluctuate from less than 25,000 to more than 100,000 per cubic millimeter, but this is significantly fewer than the 5 million red blood cells, 300,000 platelets, and 7000 white blood cells found in the same volume of human blood. With the exception of a few aquatic midges, insect hemolymph does NOT contain hemoglobin (or red blood cells). Oxygen is delivered by the tracheal system, not the circulatory system.