NATIONAL OPEN UNIVERSITY OF NIGERIA

SCHOOL OF SCIENCES

COURSE CODE: BIO 211 (2 CU)

COURSE TITLE: Coelomate Invertebrates

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Course Title **Coelomate Invertebrates**

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CONTENTS
PAGE

Introduction

BIO 211 – 'Coelomate Invertebrates' is a second semester two-credit unit core course for students studying for a Bachelor's degree in Biology and related courses.

The course covers an area of zoology/biology that deals with the study of 'higher' invertebrate groups. Another course would have earlier treated the 'lower' invertebrates. Most of the so-called 'lower invertebrates' are at the cellular and tissue levels of organisation, i.e. some are cellular (an aggregation of more or less independent cells that are not organized into tissues and organs) and some diploblastic (having two cellular body layers – ectoderm and endoderm). Note that the protozoans are no longer regarded as belonging to the animal kingdom; they are unicellular/acellular and are at the cellular level of organization. The coelomate invertebrates are neither cellular nor diploblastic, but triploblastic (consisting of three embryological cellular body layers – ectoderm, endoderm and mesoderm). The acoelomates, which although triploblastic, and have organs and systems, do not have a coelom and are included among the 'lower invertebrates'. The acoelomates are more complex than the invertebrates with the cellular and tissue grades of organization. Although the acoelomates have organ systems, they are the simplest phylum of animals built on the organ system level of construction. Starting with the flatworms, all more complex animals are bilaterally symmetrical and cephalized.

The pseudocoelomates have all the attributes of the acoelomates i.e. organ systems and, in addition, a body cavity, the pseudocoel ('false' coelom), so-called because its formation does not involve the mesoderm and therefore does not have a peritoneal lining. The coelomate invertebrates, which are covered in this course, are those that have a true coelom and are called coelomates or eucoelomates. Their body cavity, unlike that of the pseudocoelomates, involves the mesoderm and has a peritoneal lining.

The coelomate body plan is more complex than that of the acoelomates and the pseudocoelomates. With the appearance of a coelom, the body plan of the invertebrates and higher taxa became more complex and the systems more efficient. Although the coelom is very distinct at the embryonic level, it becomes modified and greatly reduced in the adults of some of the invertebrate coelomate groups.

In this course, we shall be discussing invertebrate coelomates i.e. animals that have a coelom but do not have a vertebral column.

What you will learn in this course

This course consists of course units and a course guide. The course guide gives you an overview of the course, the course materials and how to work with them. Addi-

tionally, it provides general guidelines on the amount of time you may spend on each course unit for fruitful and successful completion.
You are also given guidance regarding the Tutor-Marked Assignment, which will be included in your assignment folder. There will be regular tutorial classes on the course, which you are advised to attend.
This course will prepare you for other related courses at this and a higher level.

Course Aims

BIO 211 aims to enlighten you on the origin of the coelom and its implications. It also seeks to show you the different groups of invertebrates in which it occurs and how it has become modified in each of the groups. It is important to know that although it has become greatly reduced at the adult stage in some groups, all animals that are designated as coelomates/eucoelomates had a distinct coelom during embryonic development.
This course also aims to enlighten you on both the external (morphology) and internal (anatomy) organization of invertebrates, including biological processes that are associated with these features. It also aims to show how lifestyle differences influence their features.
In discussing this course, a systematic approach is taken i.e. studying animals according to their taxonomic groups, and aims to show you the differences between the groups according to their positions in the taxonomic hierarchy.

Course Objectives

To achieve the above aims, this course has sets of objectives, which are indicated at the beginning of each study unit. You are advised to read the objectives before going into the contents of the study units. While reading the study units, bear the objectives in mind.

You will find below, a comprehensive list of the objectives of the whole course. By meeting these objectives, you would have achieved the aims of the whole course.
After completing BIO 211, you are expected to be able to:

- ♣ Define a coelomate/eucoelomate animal.
- ♣ Learn the features of the different types of body cavities of invertebrate groups.
- ♣ Define an invertebrate and be able to distinguish it from a vertebrate.
- ♣ Recognize the major invertebrate phyla by their characteristics.
- ♣ Note the state/fate of the coelom in each of the coelomate invertebrate phyla.
- ♣ Appreciate the morphological features of the phyla and classes discussed.
- ♣ Appreciate the anatomical features of the phyla and classes of coelomate invertebrates.

- ♣ Describe the generalized forms of the phyla and subphyla of these invertebrates.
- ♣ Apply the description of the generalized forms to the recognition and understanding of the organisation of the individual classes of the phyla examined.
- ♣ Note the structural modifications of the features of the generalized forms in the classes and phyla of coelomate invertebrates.
- ♣ Learn how the anatomical features examined are adapted to the functions they perform.
- ♣ Appreciate the positive and negative impacts of the activities of the invertebrates on the environment, the economy and on humans.

Working through this course

For a satisfactory completion of this course, it is vital for you to read each study unit, the textbooks listed at the end of each unit, if accessible, or their equivalent, and other reading material that may be provided by the National Open University of Nigeria.

Each unit contains Tutor-marked assignments for assessment purposes. At the end of the course there would be a final examination. The course should take you about a total of 17 weeks to complete. Listed below are all the components of thee course, what you need to do and how much time you should allocate to each unit for successful and timely completion of the course.

This course requires that you spend plenty of time reading and understanding the contents of the study units. It is strongly recommended that you attend the tutorial sessions so that you can discuss and share problems and ideas with your facilitators and fellow students.

The Course Materials

The main components of the course are:

- ☑ The course Guide
- ☑ Study Units
- ☑ References/Further Reading
- ☑ Assignments
- ☑ Presentation Schedule

Study Units

The modules and study units of this course are listed below:

Module 1 Coelomate Invertebrates I

Study Unit 1	Body cavities of invertebrates
Study Unit 2	Phylum Annelida
Study Unit 3	Phylum Annelida *continued*
Study Unit 4	Phylum Annelida *continued*
Study Unit 5	Phylum Mollusca
Study Unit 6	Phylum Mollusca *continued*
Study Unit 7	Phylum Mollusca *continued*
Study Unit 8	Phylum Mollusca *continued*
Module 2	**Coelomate Invertebrates II**
Study Unit 1	Phylum Arthropoda
Study Unit 2	Phylum Arthropoda *continued*
Study Unit 3	Phylum Arthropoda *continued*
Study Unit 4	Phylum Arthropoda *continued*
Study Unit 5	Phylum Arthropoda *continued*
Study Unit 6	Phylum Arthropoda *continued*
Study Unit 7	Phylum Echinodermata

The first study unit in Module 1 describes the different types of body cavities found among invertebrates and explains many of the terms that you will be coming across in the later study units; these terms are associated with the formation and possession of a coelom. The second, third and fourth units discuss the body form of a representative annelid, the earthworm, which is widely distributed and therefore easily obtainable for study. It also shows most of the features that are discussed in the first study unit, such as cephalization, metamerism, a distinct coelom in the adult stage, e.t.c. It illustrates metameric segmentation at its best. The diversity, classification, organization and the vital functions, and the economic importance of annelids are also examined in these study units.

Study units 5, 6, 7, and 8 deal with the same aspects of the Phylum Mollusca as discussed under the Phylum Annelida. In these units some modification of the coelom from the annelid type and the change in body form from metameric to monomeric are noted.

In Module 2, Study Units 1 to 6 are devoted to the study of the arthropods. This might seem a large number of units to devote to the discussion of one phylum but as mentioned in the introduction to the arthropods, this is inadequate, if justice is to be done to the phylum. Two examples are selected from the vast array of arthropods and discussed. As usual, the representatives selected are very familiar and quite characteristic of their classes. One each of aquatic and terrestrial arthropods were selected for study. This phylum is the largest on the planet and contains the greatest number of successful and economically and medically important individuals. It is noted that the impressive comments that are made about the success and importance of arthropods are mostly about insects (terrestrial) and crustaceans (aquatic). The Phylum Echinodermata is discussed in Study Unit 7 of this module. The relationship between the echinoderms and chordates is highlighted and the same features as discussed for the annelids and molluscs are also discussed in relation to the echinoderms.

Each of the study units consists of 1-2 weeks' work and includes an Introduction, Objectives, Unit Content, Conclusion, Summary, Tutor-Marked Assignments and References/Further Reading. The Tutor-Marked Assignments are supposed to test you on the material you have just studied and help you to assess how much you comprehend what you have read. The Tutor-Marked Assignments will assist you in achieving the learning objectives of each of the study units.

Presentation Schedule

Your course materials have important dates for early and timely completion and submission of your Tutor-Marked Assignments and attending tutorials. You should remember that you must submit all your assignments by the stipulated time and date. You must guard against falling behind in your work.

Assessment

There are three aspects to the assessment of the course. The first is made up of self-assessment exercise, the second consists of the tutor-marked assignments and the third is the written examination/end of course examination.

You are advised to do the exercises. In tackling the assignments, you are expected to apply information, knowledge and techniques you gathered during the course. The assignments must be submitted to your facilitator for formal assessment in accordance with the deadlines stated in the presentation schedule and the assignment file. The work you submit to your tutor for assessment will account for 30% of your total course work. At the end of the course you need to sit for a final or end of course examination of about three hours duration. This examination will account for 70% of your total course mark.

Tutor-Marked Assignment (TMA)

The TMA is a continuous assessment component of your course. It accounts for 30% of the total score. You will be given four (4) TMAs to answer. Three of these must be answered before you are allowed to sit for the end of course examination. The TMAs will be given to you by your facilitator and returned after you have done the assignment. Assignment questions for the units in this course are contained in he assignment file. You will be able to complete your assignment from the information and material contained in your reading, references and study units. However, it is desirable at the degree level of education to demonstrate that you have read and researched more into your references, which will give you broader knowledge and provide you with a deeper understanding of the subject.

Make sure that each assignment reaches your facilitator on or before the deadline given, in the presentation schedule and assignment file. If for any reason you can not complete your work on time, contact your facilitator before the assignment is due, to discuss the possibility of an extension. Extension will not be granted after the due date unless under exceptional circumstances.

Final Examination and Grading

The end of course examination 'Coelomate Invertebrates' is of 3 hours duration and is worth 70% of the total course work. The examination will consist of questions, which will reflect the type of self-testing, practice exercise and tutor-marked assignment problems that you encountered previously. All areas of the course will be assessed. Use the time between finishing the last unit and sitting for the examination to revise the whole course. You might find it useful to review your TMAs and comments on them before the examination. The end of course examination covers information from all parts of the course.

Course Marking Scheme

Assignment	**Scores**
Assignments 1 - 4	Four assignments, best three marks of the four count at 10% each - 30% of course marks.
End of course examination	70% of overall course marks.
Total	100% of course materials.

Facilitators/Tutors and Tutorials

There are 16 hours of tutorials provided in support of this course. You will be notified of the dates, times and locations of these tutorials as well as the name and phone number of your facilitator, as soon as you are allocated a tutorial group.

Your facilitator will mark and comment on your assignments, keep a close watch on your progress and any difficulties you might face and give you with assistance during the course. You are expected to mail your TMA to your facilitator before the scheduled date (at least two working days are required). They will be marked by your tutor and returned to you as soon as possible. .Do not delay contacting your facilitator by telephone or e-mail if you need assistance. The following are circumstances in which you might need to contact your facilitator if necessary:

- You do not understand any part of the study or the assigned readings.
- You have difficulty with the self-tests
- You have a question or problem with an assignment or with the grading of an assignment.

You should endeavor to attend the tutorials. This is the only chance to have face to face contact with your course facilitator and to ask questions which will be answered instantly. You can raise any problem encountered in the course of your study.
To gain maximum benefit from the course tutorials, prepare a question list before attending them. You will learn a lot from participating actively in discussions.

Summary

'Coelomate Invertebrates' is a course that will provide you with knowledge that will help you understand the different levels of organisation among invertebrate animals and quantitative and qualitative development that accompany these levels of organisation. The knowledge acquired in this course can be applied to understanding how the organization of the higher animal groups, i.e. the vertebrates and their allies, and how they are adapted to their various lifestyles. Furthermore, the course exposes you to how organization is studied according to the taxonomic groupings and how the innovation of a generalized individual can be used to understand how a whole group operates. I addition, you will be able to answer questions such as listed below:

- ✓ Briefly discuss the different types of invertebrate body cavities.
- ✓ Name the two groups into which coelomates are separated on the basis of their cleavage patterns.
- ✓ Give three distinguishing characteristics of each of the groups.
- ✓ Define metamerism.
- ✓ Define tagmatization.
- ✓ List five ways in which annelids are beneficial.
- ✓ Describe reproduction in *Astacus*.
- ✓ Why are the cephalopods considered as the most sophisticated invertebrates?
- ✓ Discuss coiling and torsion in gastropods.
- ✓ Name the classes in the phylum Echinodermata.

These are only a few of the questions you should be able to answer after completing this course. You can coin questions yourself or with the assistance of your facilitator, and attempt answering them. Your questions can also form part of the material you take to your facilitator at tutorials. You should be able to find most of the answers within your course material since information were gathered from a wide range of good text books and reliable sites on the Internet.

Enjoy your studies and best wishes.

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Module 1: Coelomate Invertebrates I

Study Unit 1: Body Cavities of Invertebrates

Contents

1.0 Introduction

Coelomates are animals that have a coelom, which is a fluid-filled body cavity between two layers of mesoderm in some triploblastic metazoans. Three body plans of metazoans are distinguishable on the basis of the:

(i) absence of a body cavity (**acoelomate**)
(ii) occurrence of a false body cavity (**pseudocoelomate**) and
(iii) occurrence of a true body cavity (**coelomate/eucoelomate**).

Invertebrates are traditionally referred to as "animals without a backbone". This definition broadly includes the single-celled protozoans (animal-like protoctistans) and all other phyla of animals that do not have a vertebral column. When animals are examined and compared, many are found to have a row of internal bones along the centre of their back; these bones are called **vertebrae** and animals that possess them, **vertebrates**. Vertebrates include fishes, amphibians, reptiles, birds and mammals, and they make up about 3% of the animal kingdom.

The other 97% are animals without backbones or **invertebrates**. There are many invertebrate animals that catch our attention while many of them go unnoticed due to their microscopic size or because they live outside the general view of humans (e.g. in water, underground, in soil, e.t.c.).

Previously, you would have studied some invertebrates, which were referred to as lower invertebrates that do not have a coelom, some of them with the cellular/protoplasmic level of organisation, some with tissues, some with organs and systems without a coelom, and others with organs and systems with a pseudocoel. In this study unit, we shall introduce the coelom and study its formation and significance in the life of animals, with particular reference to invertebrate animals.

2.0 Objectives

After the completion of this learning unit, you should be able to:

- ❑ Distinguish invertebrates from vertebrates.
- ❑ Distinguish between the different types of body cavities.
- ❑ Define a coelom.
- ❑ Appreciate the significance of a coelom and some features associated with it.
- ❑ Understand the process of coelom formation.

3.0 Body cavities of animals

Although a body cavity can be any internal body space, in this course and generally in biology and zoology, it refers to the fluid-filled space between the internal organs and the body wall. The invertebrate phyla Cnidaria/Coelenterata and Platyhelminthes have a 'solid' type of body, with **mesogloea** and **mesenchyme/parenchyma** (Fig. 1.1a) respectively, between the ectoderm and endoderm. All the other phyla higher than these two have a body cavity that separates the gut from the body wall.

3.1 Types of body cavities

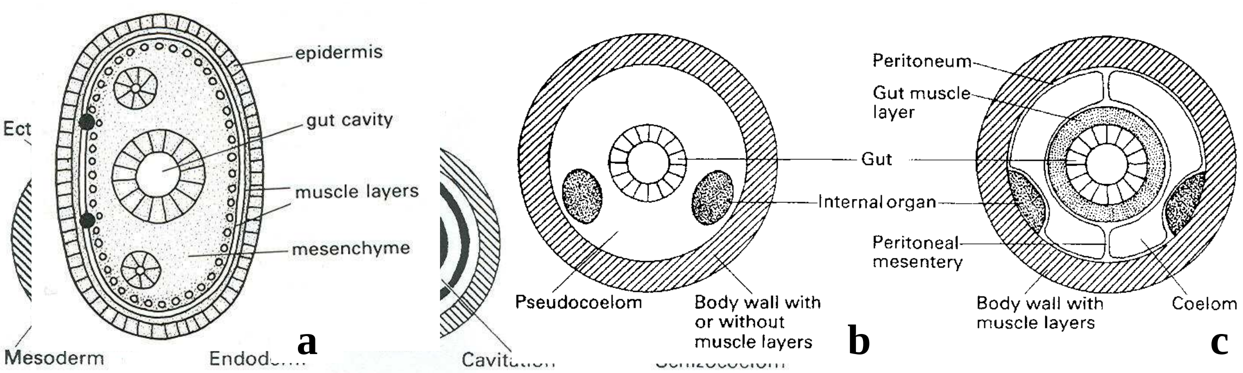
Two types of body cavities occur in animals, the less common is the **pseudocoelom** and the commonest the **coelom** and (Figs. 1.1b and 1.1c respectively). Both cavities are formed during embryonic development.

3.1.1 Pseudocoel

The first cavity to appear during embryonic development is the **blastocoel**, sometimes called the primary body cavity. The formation of a gut reduces the blastocoel, but some of the space between endoderm and ectoderm remains. It is in this part of the body (blastocoel) that the solid parenchyma of **acoelomates** (Fig. 1.1a) forms. The **pseudocoel** (Fig. 1.1b.) is a cavity left by the failure of the parenchyma to completely fill the space between the mesoderm of the body wall and the gut wall; it is a derivative of the blastocoel. No peritoneum lines the pseudocoel walls; the gut and gonads are at least partly bathed in the **perivisceral** fluid and are free within the cavity since they are not bound by peritoneum. The pseudocoel occurs between the mesoderm, which forms the muscle of the body wall, and the gut wall which is made up of endoderm. Note that the mesoderm is not involved here as is the case in the formation of the coelom, which we shall discuss shortly. The gut wall in the **pseudocoelomates** therefore has no muscle layers as in the **coelomates**. **Pseudocoelom** is found in one major phylum, the Nematoda, and a few minor phyla, the Rotifera, Gastrotricha, Kinorhyncha, Nematomorpha and Acanthocephala.

3.1.2 Coelom

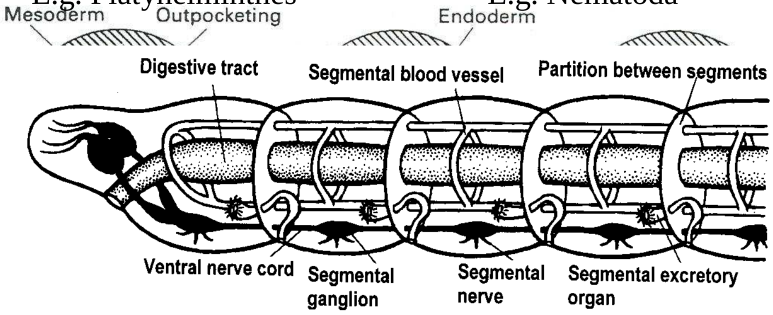
The coelom is a secondary fluid-filled body cavity that forms as a new space in the mesoderm and is completely surrounded by mesodermal tissue. The fluid in the coelomic cavity is not in direct contact with either the gut or body wall, but is separated from both by the **peritoneal epithelium** (peritoneum). The coelom forms during development in some animals by the splitting of the mesoderm due to accumulation of fluid. As the coelom increases in size, the outer part of the mesoderm becomes intimately associated with the body wall, and the body wall is lined by the parietal or **somatic mesoderm** that becomes the **parietal peritoneum** (Fig. 2a). The inner mesoderm becomes intimately associated with the gut wall and other viscera, and the coelom is lined with visceral or **splanchnic mesoderm**, which forms the visceral peritoneum. The internal organs are not actually free within the coelom but are bound by a cellular lining provided by the mesoderm in the form of mesenteries, which are actually continuations of the peritoneum (see Fig. 1.1c). The type of coelom formed by the splitting of the mesoderm is called a **schizocoel** (Fig. 1.2a). A schizocoel occurs in annelids, molluscs and arthropods. In adult molluscs and arthropods, the coelom is reduced and mostly replaced by a **haemocoel** (Fig. 1.3). The haemocoel develops from cavities of the blood vascular system and is therefore filled with blood. Blood is generally circulated in the haemocoel and through blood vessels attached to it. The coelom still exists but it is confined to the cavities of the excretory organs and reproductive ducts. The high blood volume to body volume in arthropods enables maintenance of high metabolic rate, allowing them to have a high level of activity. The coelom can also be formed from out-pocketings/ outpouchings of the mesoderm (Fig. 1.2b). Coelom formed in this manner is known as an **enterocoel**. It occurs in echinoderms, hemichordates and chordates. Most of the mesoderm that lines the coelom develops into muscle, which aids locomotion in the body wall and peristalsis in the gut wall. An important structural adaptation in coelomates is **metamerism**.



ACOELOMATE
E.g. Platyhelminthes

PSEUDOCOELOMATE
E.g. Nematoda

COELOMATE



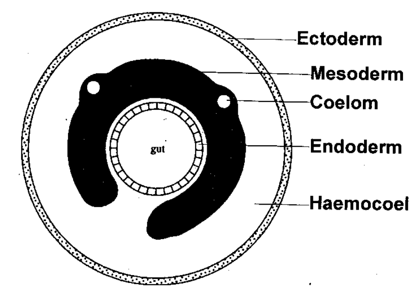


Fig. 1.3. Haemocoel. *Source*: Taylor *et al.* (1998).

3.1.3 Metamerism

This is an important structural adaptation seen in many coelomates. It is the division of the body into a series of similar segments that are developed to the same degree and arranged in a linear series from the anterior to the posterior end of the animal. Each segment may have sub-divisions of the organ systems. An 'ideal' metamerically segmented animal would have each segment with reproductive and excretory organs, as well as the skin, muscles, nerves and circulatory structures. Such an animal is however, purely hypothetical. metameric animals show specializations in these structures to a greater or lesser extent. Among the invertebrates, the annelids and arthropods are regarded as basically metameric, but the condition has been extensively modified in the arthropods that it is almost not recognizable. The annelids demonstrate the least modified form of metamerism (**refer to diagram on previous page**).

3.1.4 The significance of the coelom

a. Organs that are embedded in solid tissue (parenchyma) as in the **acoelomates** (Fig. 1a) are compressed any time the animal moves its body whereas there is freedom of movement of internal organs in animals that have a body cavity. This freedom of movement allows for efficient transportation of gut contents.
b. A body cavity provides space for the development of gonads so that eggs and sperm are stored in a constant environment. The advantage of this is that animals with a body cavity can restrict their breeding to certain times of the year that are favourable, unlike those that breed all year round. Losses of offspring would be minimized in the earlier group.
c. Fluid in the body cavity acts as a transporting medium for metabolites and excretory products. The fluid-filled cavity can also act as a hydrostatic skeleton. A hydrostatic skeleton is in contact with the muscles of the body wall and gut wall with increased mechanical efficiency and rapidity of movement.
d. Increase in size and complexity is possible in animals with a body cavity. Problems that might arise with increase in size are solved by a transport system e.g. a blood vascular system.
e. Greater complexity requires complex coordination; a more elaborate nervous system is thus formed for this purpose; **cephalization** is part of the formation of an elaborate and complex nervous system.

3.1.5 Cephalization

This refers to the development of all the features associated with the head. The development of feeding apparatus, sense organs and nervous tissue are all part of cephalization.

3.2 Protostomes and Deuterostomes

The coelomates are divided into two large groups, and many of the reasons for this separation are based on comparative embryology. Although there are exceptions to the following generalizations, most zoologists are convinced that the two groups are true evolutionary groups.

- <u>Protostome</u> - embryonic development that characterizes molluscs, annelids, and arthropods; includes four main components:

- o Spiral cleavage of the egg after fertilization. The upper tier of cells is twisted 45° out of line with the lower tier (Fig. 1.4).
- o Blastopore develops into the mouth (proto = first, stome = mouth). The indentation on the surface of a developing embryo in some animals through which the cells from the surface pass into the embryo to take their positions for further development.
- o Schizocoelous – coelom formed by splitting of the mesoderm.
- o Determinate (Mosaic) Embryo – removing a cell from the 4-cell stage results in arrested development of the embryo. Eggs whose development appears to be directed by cytoplasmic determinants localised in different parts of the egg are said to be mosaic eggs. The cells formed at the early stages of development develop independently of each other and are unable to substitute for each other if one is removed.

- Deuterostome – embryonic development that characterizes echinoderms and chordates; includes four main components that differ from protostomes.
    - o Radial Cleavage – cleavage of fertilized egg is radial. The upper tier of cells sits directly on top of the lower tier (Fig. 1.4).
    - o Blastopore develops into the anus (deutero = second, stome = mouth)
    - o Enterocoelous – coelom formed from outpouching/outpocketting of the mesoderm
    - o Indeterminate (Regulative) Embryo – removing a cell from an embryo does not affect development; the fate of the cells of the zygote is not predetermined.

Most of the coelomate invertebrate groups we shall be examining in this course fall within the first group, i.e. Protostomes; only one of the groups that we shall study later on falls within the second group (Deuterostomes). Bear this point in mind as we examine different groups of invertebrates in the units that follow.

3.3 Explanation of some terms related to the development of a coelom

3.3.1 Levels of Organization

- Cytoplasmic/protoplasmic – all life activities are carried out within the limits of a single cell membrane
- Cellular – many different functions are carried out by specific cellular structures
- Tissue – similar cells grouped together to perform common functions as a highly coordinated unit
- Organ – tissues are assembled into these larger functional units
- Organ System – different organs operate together to perform vital functions

3.3.2 Germ Layers

- Diploblastic – simplest level of tissue organization, consisting of two embryological layers: (1) ectoderm which gives rise to the epidermis (outer layer of the body wall) and (2) endoderm which gives rise to the gastrodermis (tissue that lines the gut cavity)
- Triploblastic – more complex level of tissue organization, consisting of three embryological layers: (1) ectoderm; (2) endoderm and (3) mesoderm (3 is between ectoderm and endoderm; gives rise to the organs of circulation, excretion, and reproduction plus the muscles, connective tissue, and blood cells.)

4.0 Conclusion

Invertebrate animals have no backbones, whereas vertebrates have a backbone. Coelomate invertebrates are those that have a fluid-filled body cavity that is formed from either the splitting of the mesoderm or outpocketting of outpouching of the mesoderm, during embryonic development.

5.0 Summary

Invertebrates are animals without backbones.
Coelom: A fluid-filled cavity between the body wall and the gut which is lined by mesoderm
Advantages:

- Provides more room for organ development
- Gives more surface area for diffusion of gases, nutrients and wastes into and out of organs
- Provides an area for storage
- Often acts as hydrostatic skeleton
- Provides a vehicle for eliminating wastes and reproductive products from the body
- Facilitates increased body size

  - Acoelomate – "without" body cavity surrounding the gut.
  - Pseudocoelomate – a "false" body cavity surrounds the gut but lacks a peritoneal lining;
  - Coelomate/Eucoelomate – a "true" body cavity with a peritoneal lining.
  - Schizocoel - coelom derived from the mesodermal layer through splitting
  - Enterocoel - coelom arises from outpouching of the mesodermal layer in the archenteron

The coelomates: protostomes and deuterostomes based on features in their embryology.

6.0 Tutor Marked Assignment

1. What do you understand by the term invertebrate?
2. What is a coelom?
3. Distinguish between an acoelomate, a pseudocoelomate and a coelmate/eucoelomate.
4. Name the two groups of coelomates.
5. List four differences between the two groups.

7.0 Further Reading/References

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Study Unit 2: The Phylum Annelida

Contents

Study Unit 2

THE PHYLUM ANNELIDA (ANNELIDS)

1.0 Introduction

In the last study unit, we looked at the different types of body cavities of animals, their formation and significance, with particular reference to the invertebrates. We also briefly examined some features that were associated with the occurrence of a coelom such as cephalisation, germ layers, metamerism, etc. In this, and in the next few units, we are going to study the phylum Annelida, which is one of the four major groups of coelomate metazoan invertebrates we mentioned in the last study unit.

The name Annelida is derived from the word *anellus*, which means ‘little ring’ and aptly describes the ‘ringed’ appearance of annelids. Segmentation is the key innovation for this group. The annelid worms show great advancement over the 'lower' phyla such as Cnidaria, Platyhelminthes and Nematoda. Their most characteristic feature is the **segmentation of their bodies**, both externally and internally **(metamerism)**. In some annelids, the various segments show great diversity of structure and function. Each segment is a relatively complete unit, each partitioned from the next by septa, except in leeches. Segments can be individually controlled for different functions because each segment contains its own excretory organs, and nerve concentrations that control the actions of the segment called “ganglia”. As a result of the partial septation of the coelom, hydrostatic pressure is maintained across segments and helps provide body rigidity, allowing muscle contractions to bend the body without collapsing it.

The Annelida have not only retained the basic features introduced in the acoelomates and pseudocoelomates such as triploblastic body structure, bilateral symmetry, and a body cavity, but have also made vast improvements in certain of these structures as well as contributed some new ones. The body cavity in annelids is a true coelom (surrounded by epithelial cells of mesodermal origin), the nervous system is more centralised, and **cephalisation** further accentuated. The digestive, excretory and circulatory systems are more complex and more efficient. The vascular system (a blastocoelic system) is a vast improvement over simple diffusion for transportation of oxygen, carbon dioxide, food materials, excretory materials and hormones. There is therefore a potential for greater size and complexity. Respiratory capacity is usually enhanced by the respiratory pigment **erythrocruorine** (not constrained by blood cells) in earthworms (gives approximately ten-fold increase in oxygen carrying capacity of blood). The occurrence of a mouth and an anus creates traffic of food through the digestive tract favouring the specialization of the alimentary canal for specific stages in food processing.

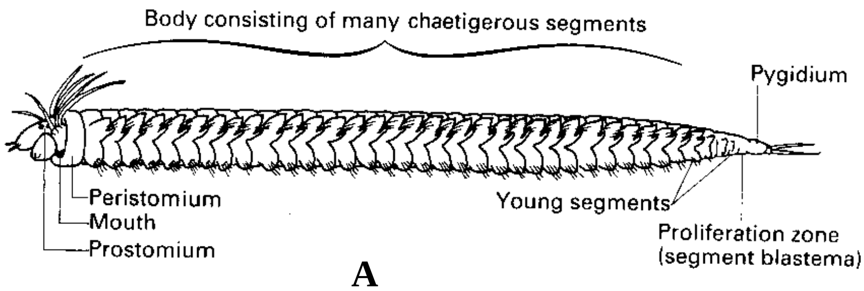
2.0 Objectives

By the end of this unit, you should be able to:

- ❑ Know the characteristics of the phylum Annelida.
- ❑ Describe annelids by their characteristic features.
- ❑ Enumerate the characteristics of the different classes of annelids.
- ❑ Appreciate the diversity of annelids.
- ❑ Appreciate the impact of the coelom and cephalisation in the life of annelids.

3.0 Diagnostic and special features of the Annelida

1. Bilaterally symmetrical, vermiform (worm-like).
2. Body more than two cell layers thick, with tissues and organs.
3. A muscular gut with mouth and anus.
4. Body divided into segments (the segmentation may not be visible externally, but is always evident in the nervous system).
5. A pre-segmental prostomium containing a nervous ganglion, and a post-segmental pygidium. (Fig. 2.1B).
6. Body cavity a series of schizocoels, obscured in specimens with anterior and posterior suckers.
7. Body cavity often subdivided by transverse septa, but frequently suppressed or obscured in some or all segments.
8. Outer epithelium covered by a cuticle and with epidermal bristles or chaetae in bundles or singly, except in specimens with anterior and posterior suckers (leeches).
9. Body wall muscular, often with complete circular muscle layers and four blocks of longitudinal muscles.
10. A closed blood system.
11. Nervous system with presegmental supraoesophageal ganglion, circum-oesophageal ring and a ventral nerve cord with segmental ganglia.
12. Segmental ducts of mesodermal and ectodermal origin, which may be combined, restricted to one or a few segments and/or partially suppressed.
13. Varying degrees of cephalization.
14. Annelids may be monoecious or dioecious.
15. Larva may or may not be present; if present it is of the **trochophore** type (Fig. 2.1B).
16. Planktonic development in marine forms sometimes via a free-living trochophore larva but this stage frequently encapsulated.
17. Some forms also reproduce asexually.
18. They are protostomes, with spiral cleavage



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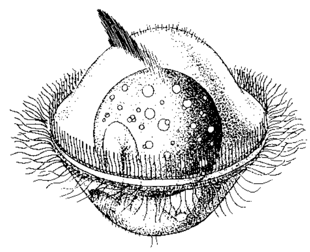


B

Fig. 2.1. **A**, The basic body regions of the annelid illustrated using the polychaete *Nereis*. **B,** Trochophore Larva of annelids. Source: Barnes *et al.*, 1989.

3.1 The diversity of annelids
There are about 12,000 species that include sandworms, fanworms, bristleworms, ragworms, earthworms and leeches. Most of them are marine, but they are also common on land and in freshwater.

3.2 Classification
There are three classes of the Annelida named on the basis of the presence or absence of chaetae and on their number and nature, as follows:

- ☞ **Class Polychaeta** these are marine worms comprising worms that are commonly called fan worms, feather worms, tube worms, bristleworms, ragworms, sandworms, etc.
- ☞ **Class Oligochaeta –** earthworms; both terrestrial and freshwater
- ☞ **Class Hirudinea –** leeches; mostly freshwater, some terrestrial and marine.

Note that some classifications place the Oligochaeta and Hirudinea together under one class called **Clitellata** and consider the former two classes as subclasses. They have been grouped together on the obvious basis of their possessing a clitellum; a clitellum is absent in the Polychaeta.

3.2.1 Class Polychaeta
The name means "many bristles", hence the common name, marine Bristle worms. There are over 5,500 species comprised of mostly marine, and a few freshwater and terrestrial species.

The class characteristics which you should be able to remember in the polychaetes are as follows:

- External and internal segmentation.
- Lateral biramous (two-branched) parapodia (fleshy paddle-like appendages) which carry many setae/chaetae (or bristles).
- The chaetae are chitinous (made up of chitin).
- Usually strongly cephalised and specialized with eyes, and head appendages (palps and tentacles).
- Absence of a clitellum.
- Separate sexes (i.e. dioecious).
- Fertilization is external.
- An important link in marine food chains.
- Many live in association with sponges, molluscs, echinoderms, crustaceans.
- They have no suckers.
- The gonads are localized but extend throughout the body.
- E.g. *Nereis, Sabella*, *Arenicola, Aphrodite, Eunice, Glycera*, etc.

The head proper is well-developed and made up of the prostomium and peristomium. The triangular prostomium projects above the mouth and bears one pair of tentacles, one pair of fleshy palps, and two pairs of eyes. The peristomium, surrounding the mouth, is the first true segment. It bears 4 pairs of peristomial tentacles. Each segment behind the peristomium is similar and each bears a pair of fleshy parapodia laterally.

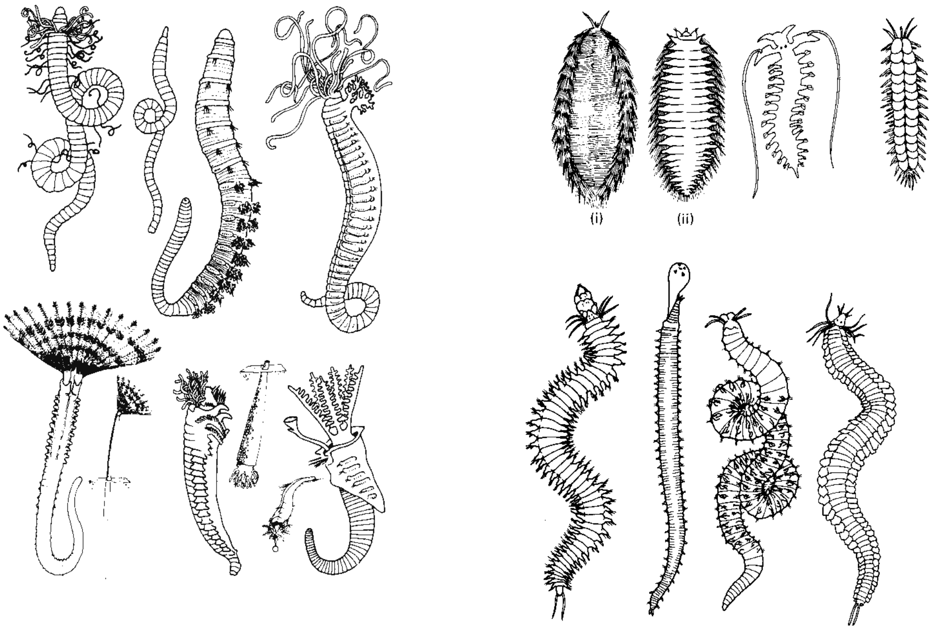


Fig. 2.2. The range of body form among polychaetes. (i) is dorsal view & (ii) ventral view. The set of 7 on the left are sedentary while the set on the right move around. The smaller illustra-tions on the left show the lifestyles of the respective polychaetes. *Source*: Barnes *et al.*, 1989

3.2.2 Class Oligochaeta (Earthworms)

The word Oligochaeta means "few bristles". There are over 3,500 known species. The oligochaetes differ from the polychaetes in that most are terrestrial or freshwater. Oligochaeta are said to have probably evolved from the Polychaeta, or at least from some common ancestor. Many of the differences between the two classes can be seen as adaptations to the burrowing terrestrial life displayed by oligochaetes. These include: reduction of the head, absence of parapodia, and greater complexity of the reproductive system.

The characteristics of the class are as follows:

- Segmented externally and internally.
- Absence of parapodia but with setae/chaetae arranged singly, arising from the body wall.
- Head usually poorly developed (prostomium simple) and lacking appendages.
- Lack eyes - but have sensory systems that detect light, touch, and moisture.
- With a **clitellum** (which secretes cocoon) and a spacious coelom.
- Hermaphroditic.
- Most species are terrestrial or freshwater.
- Usually burrow in soil.
- Have fewer setae than polychaetes.
- Eat soil and organic debris.
- Castings are deposited at surface.
- Reproduction is by copulation and cross fertilization.
- They lack suckers.
- E.g. *Lumbricus terrestris, Tubifex tubifex,* etc.

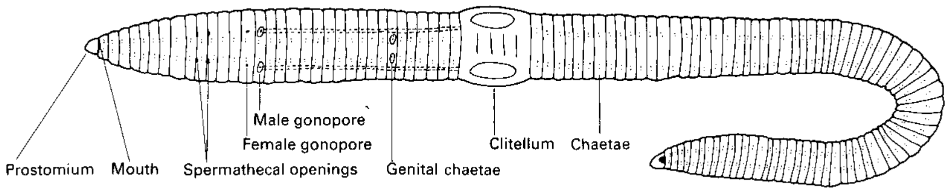


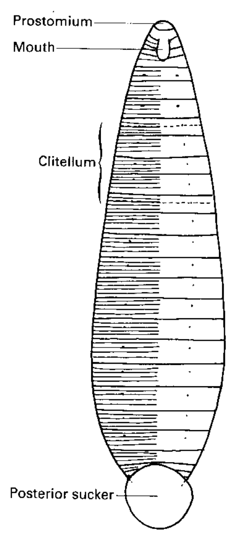
Fig. 2.3. External morphology of the earthworm *Lumbricus terrestris* in ventral view. *Source*: Barnes *et al.* (1989)

3.2.3 Class Hirudinea (leeches)

There are over 500 species of marine, freshwater and terrestrial leeches. They are mainly known for their ectoparasitic blood sucking habits, however many leeches are freshwater and marine predators. An anterior and a posterior sucker are present and correlate with restriction to a small, fixed number of segments (34). Parapodia and setae are absent and segmentation obscured by the development of secondary annuli and loss of septation. Photoreceptors light sensitive cells are usually grouped into distinct eyes. The coelom is reduced to a system of sinuses and. internal metamerism is evident only in nervous and excretory systems. They are hermaphrodites with internal fertilization, with external spermatophores or vaginal insemination.
Leeches secrete an anticoagulant termed **hirudin**, which is injected into the wound, as in some leeches; it may be reserved for preventing clotting of blood in the crop, as in *Hirudo,* which also secretes a histamine into the wound to cause dilation of the blood capillaries of the host to enhance bleeding. There are no proteolytic enzymes in the crop of *Hirudo* and digestion of blood is carried out by the symbiotic bacterium *Pseudomonas*.

3.2.4 Characteristics

- They are highly specialized annelids.
- Many are ectoparasites of vertebrates, while some are free-living predators or scavengers.
- They occur mostly in freshwater with a few on land and in the sea.
- They have anterior and posterior suckers.
- They lack a distinct head.
- Their body is somewhat shortened; all members of this class have 33/34 segments.
- They lack chaetae or parapodia or head appendages.
- They are hermaphrodites.
- Reproduction is by cross fertilization.
- Development is direct within cocoons secreted by the clitellum.
- E.g. *Hirudo medicinalis* etc.



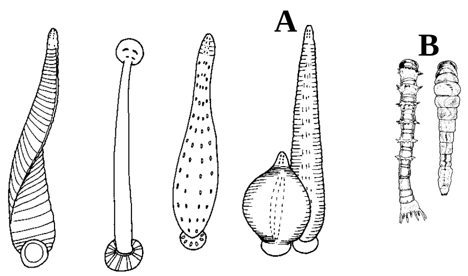


Fig. 2.4. The range of form in leeches. The two labelled **A** illustrate the great ability to change shape. **B** belong to a different subclass. *Source*: Barnes *et al.*, 1989

Fig. 2.5. The external anatomy of *Hirudo*. The external annulation is shown on the left and the true segmentation on the right. *Source*: Barnes *et al.*, 1989

Annelids are triploblastic, bilaterally symmetrical, metamerically segmentated invertebrates, with a true coelom. Except in leeches, the coelom is partially subdivided by septa.

5.0 Summary

The phylum Annelida contains triploblastic, bilaterally symmetrical, metamerically segmented, coelomate animals. Three principal features of annelids include metamerism, specialized segments, and connections between segments. Annelids may be monoecious or dioecious and reproduce asexually and sexually. Their structural design is closely related to their locomotion. The significance of the coelom appears to relate to the need for a fluid, deformable interior in animals moving by peristaltic locomotion. The phylum contains three classes: Polychaeta, Oligochaeta and Hirudinea.

6.0 Tutor Marked Assignment

1) List five characteristics of the phylum Annelida.
2) Name the classes of annelids.
3) Describe very briefly, the sort of animals that are referred to as annelids.
4) Distinguish between the Oligochaeta and Polychaeta.
5) Search for and give actual names to the illustration of body forms among the polychaetes and leeches.
6) What is/are the mode(s) of feeding in leeches?

7.0 Further Reading/References

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Study Unit 3: The Phylum Annelida *continued*

Contents

Study Unit 3

THE PHYLUM ANNELIDA (ANNELIDS) *continued*

1.0 Introduction

In the previous two study units, the formation and significance of the coelom were explained, the phylum Annelida introduced and its component classes characterised. In the last study unit, we saw how the occurrence of a coelom impacted positively on different aspects of life's processes in the annelids. Here, we are going to study organization of the bodies of the annelids, to include their organ systems and their functions. The body of an annelid is often described as a tube within a tube. The inner tube, or digestive tract, is separated from the outer tube, or body wall, by the coelom. The head region (prostomium) is followed by a series of segments similar to each other in appearance. The body in many species, especially in the sedentary polychaetes, is separated into two or three regions.

2.0 Objectives

On completion of this study unit, you should be able to:

- Appreciate the morphology of the annelids.
- Know the body plan of the annelids as demonstrated by *L. terrestris*.
- Understand the role played by some of the anatomical features of the annelids.
- Relate the anatomical structures examined to the functions they perform.
- Appreciate the significance of the coelom.

3.0 The organization/body plan of Annelids

The body plan of earthworms, as demonstrated by *Lumbricus terrestris*, is remarkably constant and will be used to illustrate the body plan of annelids. Some of the differences that occur between this species and members of the other classes will be mentioned along the way. The body plan is best illustrated in transverse section and three-dimension.

3.1 *Lumbricus terrestris* a representative annelid

Lumbricus terrestris is one of the more common annelids, occurring frequently in pasture and woodland soils which are not too acid or too waterlogged. It lies inside a burrow that may be up to two metres deep at times of cold or drought; the burrows frequently end in a small chamber. The walls of the burrows are prevented from collapsing by a cement lining of defaecated soil. The adult worm can reach a maximum length of 300 mm. The organization of earthworms and other annelids is usually described as “a tube within a tube”. In transverse section, the anterior third of its body is round, but the posterior two-thirds of the body shows some degree of dorso-ventral flattening. The body is made up of about 150 segments, with conspicuous annuli marking the positions of the internal septa (singular: septum). The **prostomium** is reduced to a small cone, and the **peristomium** to a simple segment with a ventral mouth. The chaetae, which are composed principally of the polysaccharide chitin held together with scleroprotein fibres, are very short, and project only slightly out of the skin. Each chaeta is secreted by a single cell which lies at the base of the chaetal sac. Protractor and retractor muscles associated with the **chaetae** enable them to be protracted or withdrawn. The **clitellum** is a conspicuous structure, particularly in sexually mature worms. It involves segments 32 to 36 or 37, and is formed by epidermal glandular thickening.

3.1.1 The body wall

The structure of the body wall is very similar to that of *Nereis.* A thin cuticle, consisting mainly of collagen fibres with polysaccharide and gelatin, is secreted by the epidermis which is a simple columnar epithelium with numerous mucus-secreting glands and sensory cells. Mucus secreted by the epidermis passes onto the surface of the worm through perforations in the cuticle. Sensory cells include touch and chemical receptors, which are randomly distributed through the epidermis; photoreceptors are also present. There is also a nerve net just below the epidermis. The body wall is completed by a well-developed layer of circular muscle and a layer of longitudinal muscle, which is arranged in nine blocks (six ventro-lateral, two dorso-lateral and one ventral). These muscle blocks have a very elaborate structure, and are strengthened by lamellae of collagen, which are well supplied with blood vessels. The muscle fibre is ribbon-like and composed of a single elongated cell; the cells are grouped in bundles and arranged along the sides of the lamellae. This arrangement has a feather-like appearance in transverse section, and gives the longitudinal muscle considerable strength (approximately ten times that of the circular muscle).

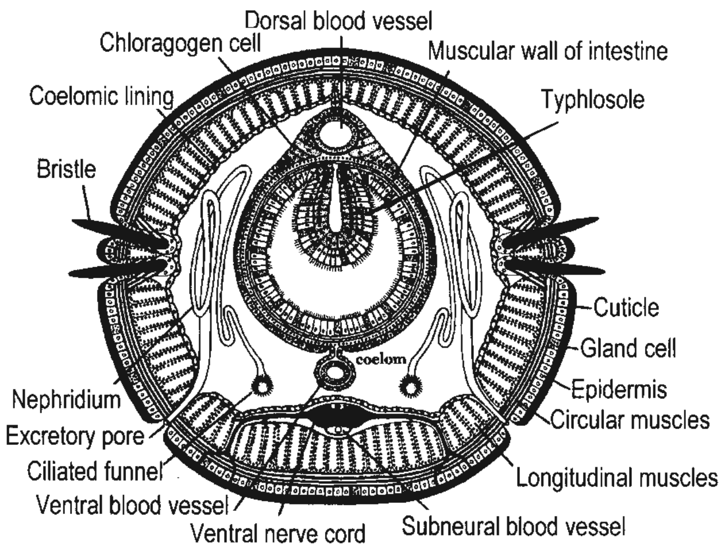

Fig. 3.1. Transverse section of an earthworm. **Bristle** in the drawing refers to **chaeta**. Each nephridium really occupies two segments: the ciliated funnel opens into the segment anterior to that which contains the body of the tube and the external pore. Only two of the four pairs of bristles are shown. *Source:* Buchsbaum *et al.* (1987) – Modified.

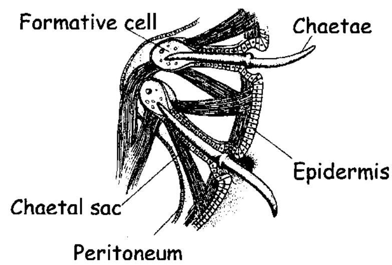

Fig. 3.2. Chaetae and chaetal sacs of *L. terrestris*. *Source:* Kershaw (1988).

3.1.2 The coelom

As mentioned under the characteristics of the oligochaetes, the coelom is completely subdivided by well-developed septa (singular: septum) with numerous bundles of circular, radial, and oblique muscle fibres. Some communication between segments is possible through a sphinctered aperture lying immediately dorsal to the nerve cord, although this is normally closed. In each segment, a sphinctered mid-dorsal pore opens from the coelom through the body wall to the exterior. Coelomic fluid can be exuded through this pore onto the skin, to provide additional surface moisture.

3.1.3 The digestive system and feeding

Lumbricus feeds on decaying fallen leaves together with the saprophytic fungi and bacteria which cause their decay. It collects these from the soil surface at night and pulls them into its burrow, while it remains anchored to the burrow by the tip of the posterior end of the body. Large quantities of soil are swallowed during feeding and also during burrowing.

The gut is simple. The mouth opens into a thin-walled buccal cavity which is slightly thickened dorsally to form a tongue. This can be protruded through the mouth and is used to pick up small pieces of vegetation. The pharynx, which opens from the buccal cavity, is the principal swallowing organ. It is a thick-walled muscular structure extending to segment 6, and has both intrinsic muscles, and radiating extrinsic radial muscles which are inserted onto the body wall. The contractions of these muscles pump food into the mouth.
The lining of the pharynx is highly glandular, with salivary glands secreting mucus to provide the necessary moisture. (Moisture-secreting glands are always present in the anterior part of the alimentary canal of terrestrial animals where no liquid is taken in with food). Glands that secrete digestive enzymes, including proteases, are also present in the pharynx, as well as in the crop and intestine.

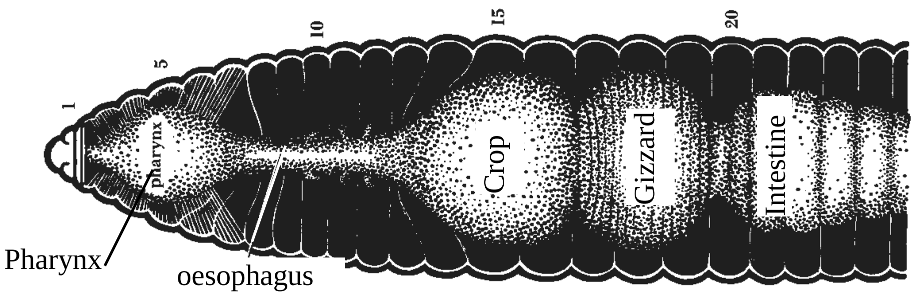

Fig. 3.3. The digestive system of *Lumbricus terrestris* showing the regions at the anterior end followed by a long uniform intestine. There are two pairs of calciferous glands in segments 11 and 12. *Source:* Buchsbaum *et al.* (1987).

The pharynx opens into the oesophagus, which is differentiated into three regions: a thin-walled tube extending to segment 13, a crop (segments 14 and 15), and a gizzard (segments 16-19). The crop is thin-walled and used as a storage organ. In contrast, the gizzard wall is tough and muscular and lined by cuticle; here, soil grains and leaf particles are ground together. This structure is an adaptation for feeding on dry matter and is greatly reduced in earthworms which have abandoned a strictly terrestrial mode of life and returned to wet or aquatic habitats.
Calciferous glands are characteristic of the oligochaete oesophagus, and are related to its burrowing habit. They are lateral evaginations of the oesophageal wall (in segments 11 and 12 in *Lumbricus)* which have no direct digestive function, but serve to remove excess calcium and carbonates taken in with the soil which could unbalance the pH of the body fluids. Excess calcium and carbonate ions are accumulated in the calciferous glands forming calcite crystals (a crystalline form of calcium carbonate) which then leave with the faeces.

A long, straight intestine completes the gut. A ridge, known as the **typhlosole** (Fig. 3.2), projects into the lumen from the dorsal surface, serving to increase the surface available for the production of digestive enzymes, (which include

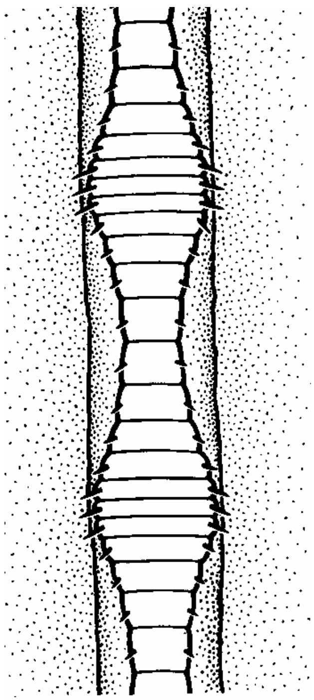

Fig. 3.4. Worm moving upward in its burrow extends or retracts the bristles of each segment as muscular waves pass down the body from head to tail. *Source:* Buchsbaum *et al.* (1987).

cellulase and chitinase), and absorption. Digestion, which is extracellular, is the primary function of the anterior region of the intestine; absorption being the main role of the posterior region. The enzymes produced within the intestine of *Lumbricus* include cellulase and chitinase, so the animal can digest the cell walls of plants and the exoskeleton' of soil arthropods. The intestine has an inner layer of circular muscle fibres and an outer layer of longitudinal muscle fibres. **Peristaltic waves** of contraction of these muscles provide mixing, and conduct food through the gut. The intestinal epithelium is ciliated; the cilia beat to facilitate mixing of the gut contents. The intestinal wall is abundantly supplied with blood vessels so that digested food is carried to the rest of the body.

In the intestinal region, the peritoneum gives rise to a dense layer of **chloragogenous cells**, which gives it a deep yellow colour (the name of the cells refers to this). These cells are thought to be involved in both nitrogenous excretion and food storage. Their position in relation to both the intestine and coelomic fluid would suit them for this. They may be shed through the nephridia. Chloragogenous cells are not restricted to *Lumbricus*, but occur in many oligochaetes and polychaetes in different regions including the oesophagus, intestine, nephridia, and principal blood vessels.

3.1.4 Locomotion

Whether crawling or burrowing, the worm proceeds by extension, anchoring, and contraction rather than by undulation. Each segment becomes alternately short and fat (by contraction of the longitudinal muscle) or long and thin (by contraction of the circular muscle). Alternating waves of contraction pass along the body from anterior to posterior, a new wave beginning as the first passes into the posterior half. The chaetae point in the posterior direction, to allow segments move forwards easily, but preventing them from sliding back. Segments in a state of longitudinal contraction protract their chaetae to anchor them to the ground; segments in which the circular muscle is contracted withdraw their chaetae and are either pulled up or pushed forward. Burrowing is similar to crawling, but the anchoring segments are pressed firmly against the wall of the burrow.

3.1.5 Blood circulatory system and exchange of gases

The blood is similar in composition to that of *Nereis*, and contains the respiratory pigment haemoglobin in solution. The circulatory system is a closed system and based on a similar plan, involving a combination of longitudinal and segmental blood vessels. The main collecting vessel is the dorsal blood vessel, which runs for most of its length in close contact with the gut. A ventral blood vessel is suspended in the mesentery ventral to the gut, and in addition, three important longitudinal vessels, a median sub-neural vessel and paired, lateral neural vessels are found in association with the nerve cord. Circulation is brought about by the contraction the dorsal blood vessels passing in waves from the anterior to the posterior waves, coupled with dorsal to ventral waves of contraction of five large commissural vessels (the pseudohearts), in segments 7 to 11. Additional control of the blood flow is provided by a system of passive valves in the vessels.
The dorsal vessel receives blood from the body wall via segmental parietals, and from the gut via three vessels per intestinal segment from the **typhlosole** and two from the gut plexus capillaries. In all segments, except the anterior 11 it is connected to the sub-neural vessel by a pair of dorsosubneural vessels which run in the septa. Longitudinal extensions from each of the anterior dorso-subneurals, and the lateral oesophageals, collect blood from the oesophagus and pharynx.

The ventral blood vessel is the principal route of distribution, giving off five main vessels in each segment. A pair of ventro-parietals extend to the body wall, and three ventro-intestinals to the gut plexus. The nephridia and reproductive organs are supplied with blood by small branches from the ventro-intestinal vessels. Blood is supplied to the nerve cord by branches of the lateral neural vessels, and collected from it by the sub-neural vessel.

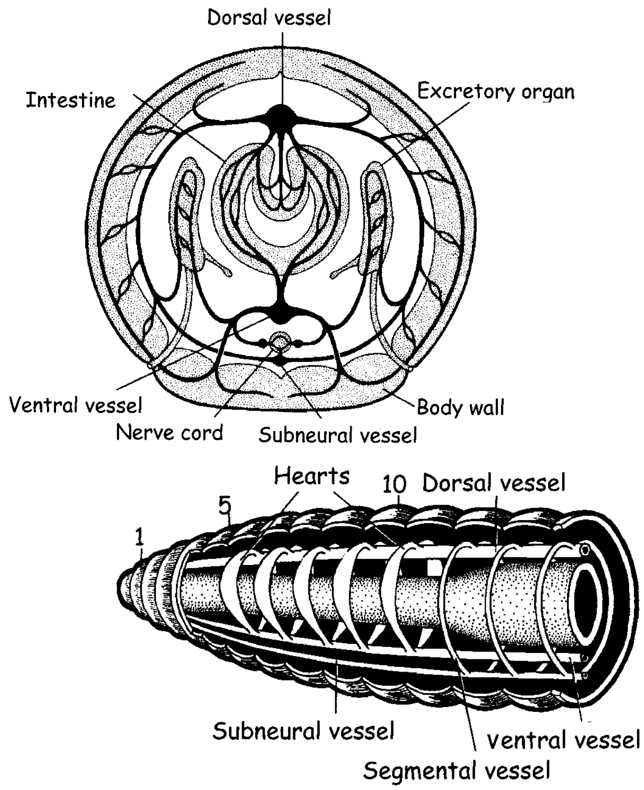

Fig. 3.5. Left, The main segmental blood vessels of an earthworm shown in transverse section. **Right,** Anterior circulatory system of an earthworm (3D). Blood flows forward in the dorsal vessel and downward through the five pairs of hearts into the ventral vessel. In front of the hearts, blood flows forward in both dorsal and ventral vessels to the head, then backward in a sub-neural vessel. Behind the hearts, blood flows backward in the ventral vessel and out into the segmental branches. *Source:* Buchsbaum *et al.* (1987).

3.1.6 Respiration

In some annelids, including earthworms, gaseous exchange takes place by diffusion over the general body surface, the necessary moisture being provided by exudations of the coelomic fluid through the dorsal pores, by the secretions of epidermal mucous glands, and by excretions from the nephridia. The extensive subepidermal capillary network is supplied with blood from the ventral vessel via the ventro-parietals and drained into the dorsal vessel via the segmental-parietals. However, many polychaetes and some clitellates (the name by which earthworms and leeches are called because they have a clitellum) have gills associated with most segments, often as extensions of the parapodia in polychaetes. In tube-dwellers, the gills aere usually more concentrated at the end that is exposed to stronger water currents.

4.0 Conclusion

The organization of the body of the annelid as shown by *Lumbricus* forms the appearance of a tube within a tube which can be observed in transverse section.

5.0 Summary

The organisation of the body is described as a tube within a tube.
The body wall of annelids is made up of cuticle, an epidermis and one band each of circular and longitudinal muscle. Each seta is a bristle-like rod set in a sac and moved by tiny muscles.
Setae anchor segments during burrowing. Earthworms move by peristalsis.
Most oligochaetes are scavengers, feeding on decayed organic matter, leaves, refuse, etc.
Food is moistened by the mouth and drawn in by a sucking action of the muscular pharynx.
The typhlosole increases surface area for absorbtion. Chloragogen tissue surrounds the intestine and synthesizes glycogen and fat.
Coelomic fluid and blood carry food, wastes and respiratory gases.
Earthworms have no special gaseous exchange organs; the moist skin handles all exchanges.
Blood circulates in a closed system.

6.0 Tutor Marked Assignment

1) How is the organisation of the annelid's body generally described and why?
2) What is the typhlosole and what is its function?
3) What does the earthworm feed on?
4) Name the main compartments of the digestive tract and state their different functions.
5) How is blood circulation brought about in Lumbricus?
6) Name the principal route of blood distribution.

7.0 References/Further Reading

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Study Unit 4: Phylum Annelida *continued*

Contents

Study Unit 4

THE PHYLUM ANNELIDA (ANNELIDS) *continued*

1.0 Introduction

This study unit is a continuation of the study of the body plan of annelids, which we started to examine in the previous unit. In the last unit, we studied some aspects of the organization of the body of annelids, using the common earthworm, *Lumbricus terrestris* as an example of a typical annelid. We chose *Lumbricus terrestris* for study because it is simple and ubiquitous. In unit 3, we looked at the general body plan, the structure of the body wall, the coelom, feeding and the digestive tract, and locomotion. In this unit, we shall examine the excretory and nervous systems, sense organs, reproductive system, reproduction, and the economic importance of annelids.

2.0 Objectives:

By the end of this study unit you should be able to:

- ❑ Appreciate the structure of the excretory and nervous systems of annelids.
- ❑ Understand how impulses are transmitted in annelids.
- ❑ Know how *Lumbricus* senses changes in its environment.
- ❑ Learn how reproduction occurs.
- ❑ Appreciate the value or otherwise, of annelids to humans.

3.0 The Organisation/body plan of Annelids *continued*

3.1 The Excretory system

The basic units of the annelid excretory system are either protonephridia (singular nephridium), which have tubules (solenocytes) that end blindly within cells, contain flagella (whip-like projections), and are joined to a common duct that drains to the outside; or metanephridia, which are funnel-shaped structures containing cilia (short, hairlike processes) that open to the outside.

In *Lumbricus*, one pair of nephridia that closely resemble those of *Nereis*, are present in every segment except the first three and the last. However, the nephridial tube is extremely elongated, and divided into distinct regions; an anterior narrow tube, a middle tube and a wide tube. An elongated, posterior, muscular bladder leads to the nephridiopore which opens on the ventro-lateral surface (see Fig. 3.1 in unit 3; Fig. 4.1 below). Considerable reabsorption of proteins, water and certain essential salts and ions (including potassium, sodium, and chloride) is thought to take place in the middle and wide tubes.

Ammonia is the chief nitrogen-containing end product of protein metabolism in aquatic annelids; earthworms, adapted to living in the soil, excrete more of another nitrogen-containing compound, urea, probably as part of a mechanism to control salt and water balance in the worm. Part of the ammonia excreted by leeches may come from bacteria in part of the leech's excretory system (nephridial capsules). The ability of leeches to withstand high concentrations of ammonia is believed to result from a protective effect provided by high levels of calcium in their cells.

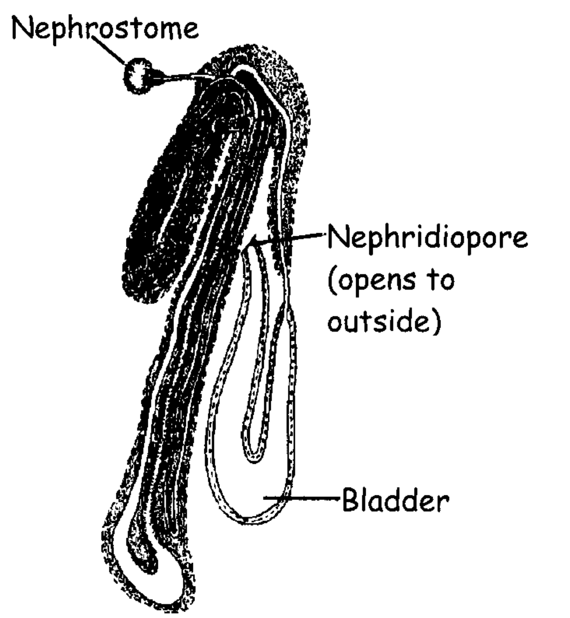

Fig. 4.1. Nephridium of *Lumbricus terrestris. Source:* Barnes (1980)

Three aspects of nephridial function in annelids corres-pond to those of the vertebrate kidney filtration, reabsorbtion, and secretion. Coelomic fluid filters through solenocytes. The ciliated funnels of meta-nephridia retain minute par-ticles and those of moderate size. In oligochaetes, whose coelomic fluid contains pro-teins, particles are actively absorbed in the ciliated region of the tubule. The tubules of earthworms also reabsorb inorganic ions such as sodium and calcium and can selec-tively eliminate excretory products from both the coe-lomic fluid and the bloodstream.

3.2 Nervous system and sense organs

This is built on the same general plan as that of the polychaete *Nereis.* A bilobed cerebal ganglion or 'brain' lies dorsal to the anterior end of the pharynx and is connected by a pair of circumpharyngeal commissures to the bi-lobed subpharyngeal ganglion, and from there to the paired ventral nerve cords. In *Lumbricus,* however, the 'brain' lies slightly more posteriorly than in *Nereis,* in the third segment. Segmental ganglia, associated with the ventral nerve cord occur in approximately the centre of each segment; those at the posterior end are particularly prominent. Three pairs of nerves are normally given off in each segment. Exceptions are the prostomium and peristomium receive nerves from the cerebral ganglion and sub-pharyngeal ganglion, respectively.

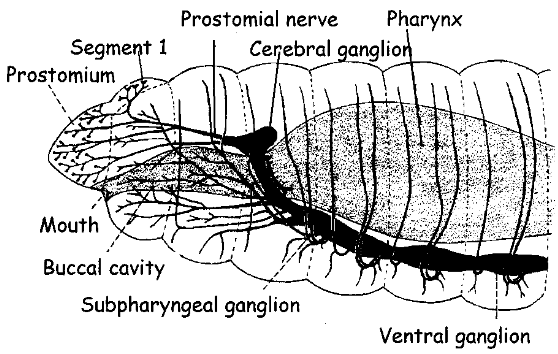

Fig. 4.2. Lateral view of the nervous system of *Lumbricus. Source:* Barnes (1980).

The polychaetes have giant fibres in addition to the arrangement of nerves just described. *Lumbricus* has five giant fibres; three are large and medially placed on the dorsal side of the nerve cord, and two are smaller, ventrally placed, and more widely separated. They innervate the longitudinal muscles through giant motor neurons arising in each ganglion, and cause all the longitudinal muscles to contract simultaneously, bringing about a sudden rapid shortening of the worm; this provides an effective escape reaction.

Many studies have been carried out on the relationship between the nervous system and behaviour in *Lumbricus.* It has been demonstrated that if the ventral nerve cord and body wall are cut, the muscles below the cut do not contract. However, if the body wall is then stitched together, waves of contraction can pass through the cut in a coordinated manner. This is possible because of local reflexes between the segments. If the longitudinal muscles are stretched, sensory cells within the muscle blocks (proprioreceptors) are stimulated, and these in turn stimulate the circular muscle to contract in the succeeding segment and so stretch the longitudinal muscles in that segment. In this way, co-ordinated waves of contraction can pass along the length of the worm.

3.3 Sensory structures

Oligochaetes lack sensory appendages and obvious eyes but they are capable of showing a range of responses to environmental conditions. Their sense organs are relatively simple in structure, consisting of single epidermal sensory cells, or groups of cells. The most common types are:

3.3.1 Touch receptors

They consist of single cells, each with a short hair-like projection through the cuticle; these may be extremely numerous (up to 1,000 per segment) and are highly concentrated on the prostomium and last segment. These cells are said to be also sensitive to changes in **temperature.**

3.3.2 Photoreceptors

They are concentrated in and below the epidermis of the prostomium. Some also occur generally over the dorsal surface of the body. Each is derived from a single cell and has a small transparent lens which focuses light onto a neurofibril network. They are most abundant in those regions most frequently exposed to light, the anterior and posterior ends, and are absent from the ventral surface.

3.3.3 Chemoreceptors

Formed from clusters of sensory cells. They are in the form of tubercles and occur in groups of three rings round each segment. In *Lumbricus* they are particularly concentrated on the prostomium, where as many as 700 per sq mm have been reported.

The ability to detect vibrations transmitted through solid objects is very important for an animal that lives underground and the earthworm has been shown to be very responsive to this. Worms are said to emerge from their burrows as a result of vibrations. They have no **statocysts** to sense gravity. Earthworms do not respond to sound. Earthworms generally move away from light, and emerge onto the soil surface at night. They also tend to move towards moisture, burrowing deeper in times of drought.

3.4 The reproductive system

The reproductive system of an earthworm is located in the anterior end, each organ in a particular segment. The male gametes are formed in two pairs of testes, located in segments 10 and 11, and each pair is enclosed within a testis sac. The testis sacs communicate with sperm sacs in which the gametes develop to maturity. Mature sperm pass back into the testis sacs, into the sperm funnels, and through the sperm ducts to the two male genital openings on the ventral surface of segment 15. Two pairs of small sacs, the sperm receptacles, in segments 9 and 10, open through pores to the ventral surface; during mating these receive sperm from the other worm. Eggs are formed in a pair of ovaries in segment 13. As they become mature, they are shed from the ovaries into two egg funnels on the posterior face of segment 13. Each funnel leads into an egg sac, in which ripe eggs are stored. The oviducts open by two pores on the ventral surface of segment 14. This diagram is based on *Lumbricus terrestris;* in some other species, certain of the details are different.

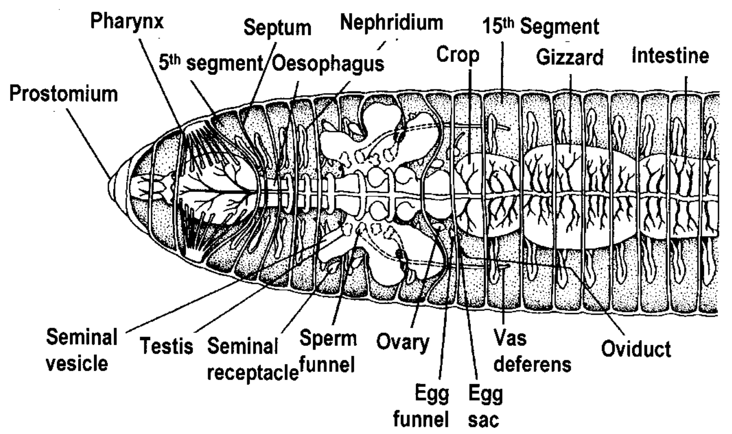

Fig. 4.3. Anatomy of *Lumbricus terrestris* showing the Reproductive and digestive systems. *Source:* Barnes (1980).

The reproductive system of earthworms is complex and fers in several respects from that of most marine annelids. To begin with, earthworms are **hermaphroditic**, a condition that is common in animals that only meet occasionally and mostly by chance. When two animals do happen to meet, reciprocal exchange of sperms can occur. The complexity of the earthworm reproductive system results partly from arrangements to keep the eggs and sperm of each individual separate and prevent self-fertilization. In addition, earthworm reproduction is modified for life on land, where the gametes and the developing embryos must be protected against drying.

3.4.1 Mating/Copulation

Mating is not a simple process for earthworms. During the sexual season, when the ground is wet following a rain, the worms may emerge at night and travel some distance over the surface before they mate. Where they are abundant, they merely protrude the anterior end and mate with a worm in an adjoining burrow. With their heads pointing in opposite directions, the two worms bring the ventral surfaces of their anterior ends together. Mucus is secreted until each worm becomes enclosed in a mucus sheath that extends from the openings of the sperm receptacles (segments 9 and 10) to the posterior edge (segment 37) of the **clitellum**, which is opposite the sperm receptacles of the partner during mating. Sperm are expelled from the openings of the sperm ducts (segment 15) and are moved backward in longitudinal grooves (roofed over by the mucus sheath) until they reach the region of the clitellum and are passed into the sperm receptacles of the other worm. All that has now happened is exchange of sperm between two worms. The worms then separate; egg laying and fertilization would take place later.

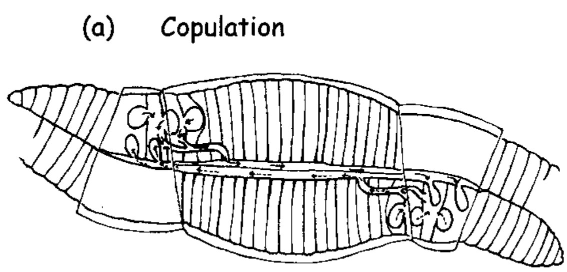

Fig. 4.4. (a) Mutual exchange of sperm between two worms; sperm are transferred from seminal vesicles to seminal receptacles as shown by the arrows. **Right**: A photograph of mating earthworms with their ventral surfaces apposed for exchange of sperm. *Sources*: Barnes *et al.* (1989); Buchsbaum *et al*. (1987)

3.4.2 Egg-laying and fertilization

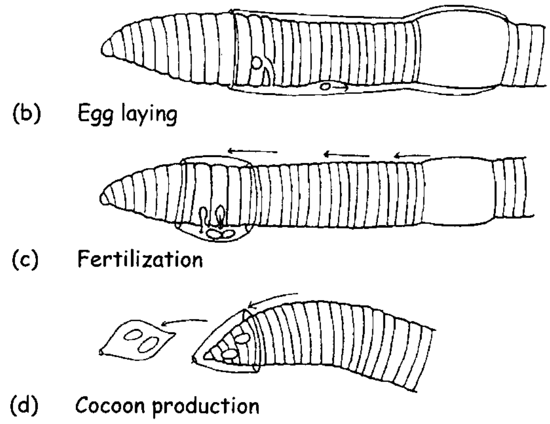

Fig. 4.5. (b) A mature egg is released from the female genital duct and passes back to the clitellum. **(c)** The cocoon secreted by the clitellum around a few eggs passes forward and the eggs are fertilized as the cocoon passes the opening of the seminal receptacle. **(d)** The cocoon containing the developing embryos is deposited in the soil. *Source*: Barnes *et al.* (1989).

At the start of egg-laying, the clitellum produces a ring of secretion, which quickly hardens, and the worm begins to wriggle backwards out of it. As the ring passes the openings of the oviducts (segment 14), it receives several ripe eggs; and then, as it passes the more anterior openings of the sperm receptacles (segments 9 and 10), it receives sperms that were deposited there previously by another worm during mating. Fertilization of the eggs takes place within the ring, which finally slips past the anterior tip of the worm and closes at both ends to form a sealed egg capsule called a cocoon. Zygotes develop directly into young worms within the capsule, buried in the soil; the young worms finally escape into the outside world.

3.5 Asexual Reproduction in the annelids

Asexual reproduction by fragmentation and budding off new individuals while the parent remains intact, occurs in a few sedentary polychaetes. It is common in aquatic oligochaetes and sexual reproduction is virtually unknown in certain species. Some oligochaetes divide to form a chain of two or more individuals which break off as young worms. Some are also capable of self fertilization and **parthenogenesis** (production of young without fertilization). Asexual reproduction in oligochaetes is always by dividing into two or more pieces, rather than by budding. Leeches have never been observed to reproduce asexually.

3.5.1 Regeneration

Annelids are said to be highly organized animals with the power of complete regeneration. The power of regeneration is shown in the polychaetes and a few oligochaetes; leeches are incapable of regeneration.

3.6 Some reproductive phenomena in polychaetes

Most polychaetes shed their gametes into the water. Various major body changes may precede the emission of gametes, the two most profound being **epitoky** (maturation into a modified, fertile form) and **stolonization** (the development of stemlike growths). At sexual maturity these polychaetes leave their burrows and swim in groups (**swarming**) before releasing gametes.

3.7 Economic importance of annelids

- The casting and the open channels created by burrowing ease the downward growth of roots and enhance the fertility of the soil by increasing aeration and drainage
- Thoroughly ground soil and secretions from the gizzard act as cement to hold soil particles together, improving soil structure and reducing erosion by compaction of soil.

- Leaves pulled into earthworms burrows are broken down by microorganisms, releasing nutrients such as nitrates, phosphates, potassium and magnesium that can be absorbed by plants.
- Earthworms and ragworms are used as fish bait.
- Ragworms are used as a food source in aquaculture.
- Some polychaetes are mollusk predators causing serious losses aquaculture and fisheries.
- The rear end of the Palolo worm (*Eunice*) that detaches for spawning is a Samoan delicacy.
- Aquatic oligochaetes are important food for fishes; a few are ectoparasites.
- Scientists study aquatic annelids to monitor the oxygen content, salinity and pollution levels in fresh and marine water.
- Burrowing species increase the penetration of water and oxygen and water into the sea-floor sediment, which encourages the growth of populations of bacteria and small animals alongside their burrows.
- Earthworms are important prey for birds, and mammals, and in some cases conserving earthworms may be essential for conserving endangered birds
- Some small tube-dwelling oligochetes transmit protozoan parasites that cause whirling disease in fish.
- Leeches can be used medically to bring circulation to areas of the body that have very poor circulation after an injury. Improved circulation prevents gangrene.
- The anticoagulant secreted by leeches keeps the circulation in injured limbs and digits from forming adhesions during the healing process.
- The anticoagulant and clot-digesting properties of substances secreted by leeches make them potentially useful as drugs for the treatment of cardiovascular diseases.
- Recently leeches have been used to assist in microsurgery, and their saliva has provided anti-inflammatory compounds and several important anticoagulants, one of which also prevents tumors from spreading.
- Leeches are vectors of fish trypanosomes (Sanguinicolidae).
- Ragworm jaws are made of unusual proteins that bind strongly to zinc and are strong but much lighter than the hard parts of many other organisms, which are biomineralized. This has attracted the attention of engineers.

4.0 Conclusion

Annelids have well-developed excretory, nervous and reproductive systems. The sensory structures of the polychaetes are generally better developed than those of the clitellates. The ability of the oligochaetes to sense their environment is limited. Annelids are important in agriculture, aquaculture, medicine and environmental studies.

5.0 Summary

The excretory system of annelids is made up of protonephridia. The chief product of protein metabolism is ammonia. The nervous system is made up of a bi-lobed ‘brain’ and nerves. Sensory cells include touch-, photo- and chemo-receptors. The earthworm is most responsive to vibrations. Although earthworms are hermaphrodites, cross fertilization is preferred. The polychaetes and oligochaetes are capable of regeneration and asexual reproduction but the hirudineans are not. Annelids are valuable in agriculture, aquaculture, medicine and environmental studies. They are also used as food by humans and wildlife.

6.0 Tutor Marked Assignment

1) Name the chief excretory products in aquatic annelids.
2) Name the sensory structures found in annelids.
3) How do annelids respond to sound?

4) Describe very briefly, the process of fertilization in annelids.
5) List three ways in which annelids are beneficial to humans
6) List three ways in which annelids cause harm to humans.

7.0 Further Reading/References

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Study Unit 5: Phylum Mollusca (Molluscs)

Contents

Study Unit 5

THE PHYLUM MOLLUSCA (MOLLUSCS)

Latin: *molluscus,* a soft nut or soft fungus

1.0 Introduction

The phylum mollusca is rather difficult to define since many of the living groups bear very little resemblance to each other, as we shall see when we examine them. Their relationship can only be traced through fossil records, which, unfortunately because they are soft-bodied, are not readily available. They are unsegmented and have a well-developed muscular locomotory organ, the foot, and fold of the dorsal wall called a **mantle**; most of them also have an exoskeleton in the form of a calcareous shell **secreted by the mantle**. Most possess a specialised feeding organ (**radula**). In other ways, molluscs follow the higher invertebrate plan in being triploblastic, with bilateral symmetry and with all organ systems. The **coelomic cavity** is reduced and often replaced by a system of **blood sinuses**. Aquatic forms have gills for respiration. The molluscs are a distinctive and individual phylum without any close resemblance or phylogenetic affinity to any other living group, except that they have retained a number of features indicative of their flatworm ancestry. However, the majority of species have departed radically from the flatworm body form and lifestyle. Molluscs are said to be very successful due to their radiation into many morphological forms.

It has long been the common practice to study the molluscs using the generalized description of an ancestral mollusc, based on a comparative study of primitive living forms. This description is purely hypothetical because no such creature is known to have existed, but it will help us understand many of the features of the molluscs.

The molluscs constitute the second major group of coelomate invertebrates that we shall be studying. In study units 2-4 we examined the organization of the annelids and some aspects of their biology and economic importance. In this study unit, we shall introduce a familiar group of coelomates belonging to the phylum Mollusca, and examine their diagnostic and special features, first of all using the ‘hypothetical ancestral mollusc’ and then their diversity and classification.

2.0 Objectives

By the end of this study unit, you should be able to:

- Appreciate the body plan of the ‘Hypothetical Ancestral Mollusc’ and its application to understanding the body organization of present day forms.

- ❑ Know and identify the characteristics of the phylum Mollusca.
- ❑ Know and identify the characteristics of **four** of **eight** of the classes of the phylum Mollusca.
- ❑ Appreciate the extent of diversification within the phylum Mollusca.

3.0 The basic body plan of molluscs

A description of the features of the 'hypothetical ancestral mollusc' that was mentioned in the introduction is as follows:

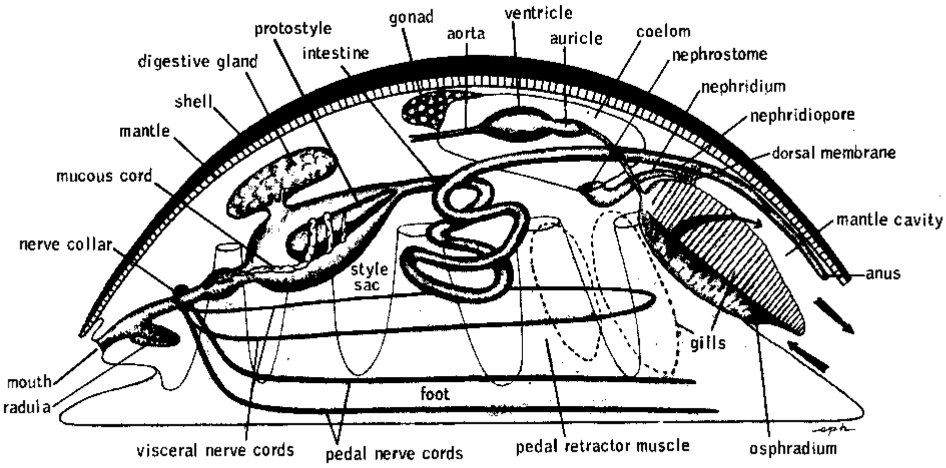


Fig. 5.1. The 'Hypothetical Ancestral Mollusc'. *Source:* Barnes (1980)

- ☞ It was thought to have lived in shallow pre-Cambrian seas, crawling over rocks and feeding on algae.
- ☞ Small in size.
- ☞ Bilaterally symmetrical.
- ☞ Oval in shape.
- ☞ Shell was low, conical and a little more than tough cuticle.
- ☞ Clamped down on rock surface, covering body as defence against predators.
- ☞ Crawled by means of a muscular foot with ciliated cells and mucous glands on its ventral surface.
- ☞ Combination of ciliary action and rippling muscle contractions within the foot brought about a slow gliding movement.
- ☞ Thought to have fed on small particles of vegetable matter, probably algae, which it scraped off the rock surface with a rasping action of its radula, a characteristic feeding structure of modern molluscs.
- ☞ Salivary glands produce mucus which both lubricates the radula and entangles the food particles.
- ☞ The anterior part of the stomach, the style sac, has a ciliated lining, with the cilia all beating at right angles to its longitudinal axis causing strings of food and mucus to rotate, to form central mass known as the protostyle.
- ☞ The alimentary canal is completed by a long intestine, in which faecal pellets formed are swept away by respiratory current.

- The gills/ctenidia were respiratory structures probably similar to those of primitive living gastropods and bivalves, with a central flattened axis projecting from the body wall and rows of broad, wedge-shaped, ciliated filaments on either side (bipectinate gills).
- The kidneys of the 'ancestral mollusc' were probably similar to annelid nephridia, with a nephrostome, tubular duct, and nephridiopore (as we saw earlier in the Annelida).
- In 'ancestral mollusc', eggs or sperm produced by the gonads may have been released into the body cavity to leave via the nephridia.
- Present day molluscs have an open blood system, the coelom being restricted to a pericardial and perivisceral structure. The typical molluscan heart consists of a ventricle with a pair of auricles opening into it. Blood enters the auricles from the ctenidia and passes into the ventricle, and then leaves the heart by a single aorta which branches to supply sinuses in which the organs are bathed directly. The 'Ancestral mollusc' is thought to have been organized in a similar way.
- The basic plan of the molluscan nervous system consists of a circum-oesophageal nerve ring with two pairs of longitudinal nerves extending posteriorly. The more ventral pedal cords innervate the foot while the dorsal visceral cords extend to the viscera and mantle. 'Ancestral mollusc' is thought to have conformed to this plan.
- The sense organs of 'ancestral mollusc' may have been similar to those of primitive living molluscs: normally eyes, statocysts and osphradia (chemoreceptors positioned on the posterior margin of the gill membranes).

3.1 Basic and special features of the phylum Mollusca

1. Bilaterally symmetrical.
2. Body more than two cell layers thick (triploblastic), with tissues and organs.
3. A through gut.
4. Without a body cavity other than provided by blood sinuses.
5. Body **monomeric** and highly variable in form, but basically squat and often conical, frequently elongated in the dorsoventral plane to form a 'visceral hump'; essentially with an anterior head bearing eyes and sensory tentacles, a large flat ventral foot, and a posterior mantle cavity, but all of these subject to considerable modification.
6. A protective, external dorsal shell of protein (conchiolin) reinforced by calcareous spicules, or from one to eight calcareous plates, secreted by the dorsal and lateral epidermis (**the mantle**); sometimes shell secondarily reduced, covered by tissue, or lost, and sometimes enlarged so as to cover whole body
7. A toothed, chitinous, tongue-like ribbon, the **radula**, can be protracted from the buccal cavity through the mouth for feeding.

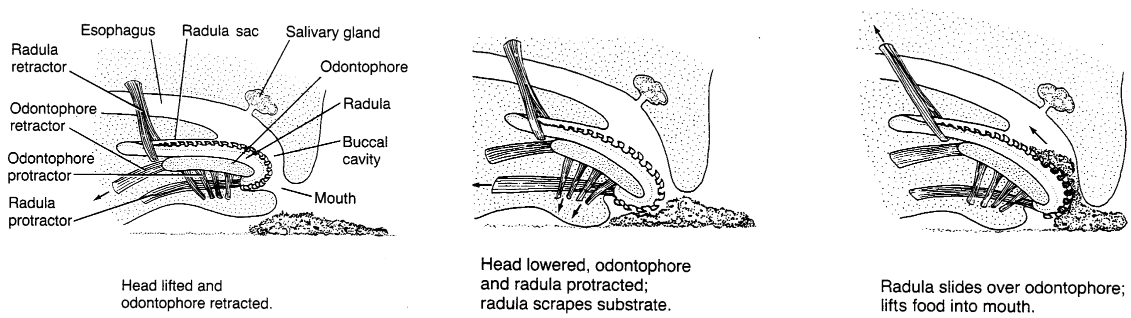
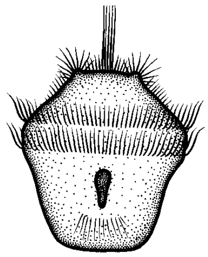


Fig. 5.2. Molluscan feeding by radular scraping and rasping. *Source:* Mitchell *et al.* (undated).

8. Gaseous exchange effected by one or more pair(s) of ctenidia/gills housed in the mantle cavity (sometimes lost).
9. An open blood system (blood does not flow through a continuous system of discrete vessels but through blood spaces surrounding organs) and a heart enclosed within a mesodermal cavity, the pericardium, through which the intestine also passes.
10. A pair of sac-like 'kidneys', open proximally into the pericardium and discharging into the mantle cavity.
11. Nervous system with a circum-oesophageal ring and two pairs of ganglionated longitudinal cords, sometimes highly concentrated.
12. They typically have a single pair of gonads that open into the mantle cavity, primitively via the pericardium and kidneys.
13. Spiral cleavage of eggs.
14. Development indirect, via **trochophore** and **veliger** larval stages or secondarily direct.



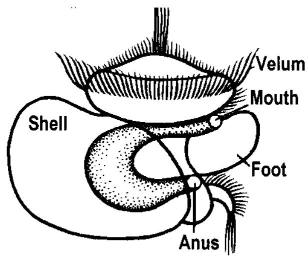


Fig. 5.3. Left, A mollusc Trochophore larva **Right,** A mollusc Veliger larva. *Source*: Buchsbaum *et al*. (1987)

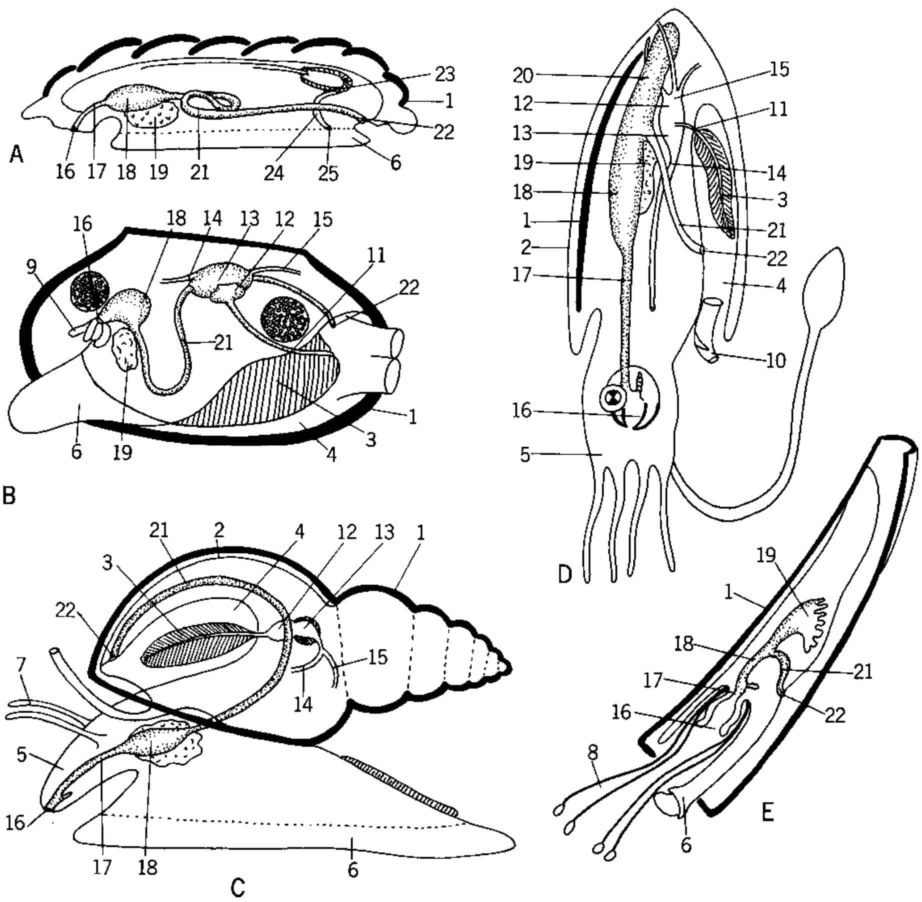


Fig. 5.4. A comparison of the organization of different major types of molluscs

KEY: *External features:* 1, shell; 2, mantle; 3, gill; 4, mantle cavity; 5, head; 6, foot; 7, tentacle; 8, captaculum; 9, labial palp; 10, siphon. *Circulatory system:* 11, gill vein; 12, auricle; 13, ventricle; 14, anterior aorta; 15, posterior aorta. *Digestive system:* 16, mouth; 17, esophagus; 18, stomach; 19, digestive gland; 20, caecum; 21, intestine; 22, anus. *Excretory system:* 23, nephrostome; 24, nephridium; 25, nephridiopore. *Source*: Meglitsch (1972).

The **Polyplacophora** (A) have a flattened form and shell composed of eight valves arranged longitudinally. The **Bivalvia** (B) have a bivalve shell, with a dorsal hinge. In the **Gastropoda** (C), the visceral mass has become very tall and extends into the usually spiraled shell. In **Cephalopoda** (D) also the visceral mass has become very tall, with the shell enclosed within the mantle. In **Scaphopoda** (E), the conical shell is open at both ends.

3.2 Diversity of molluscs

With over 100,000 named species divided between eight classes, the phylum Mollusca ranks second to the phylum Arthropoda.

3.3 Classes and Characteristics

Classification of molluscs is based on the characteristics of the foot, mantle, shell, radula and respiratory organs; based on these features, there are **eight classes** as follows:

a) Chaetodermomorpha (Aplacophora)
b) Neomeniomorpha (Aplacophora)
c) Monoplacophora
d) Polyplacophora
e) Scaphopoda
f) Gastropoda
g) Bivalvia
h) Cephalopoda

3.3.1 Class Chaetodermomorpha (solenogasters; Aplacophora)

70 species are known. They live head-down in their burrows, in soft marine sediments. Their posterior end bears a pair of ctenidia which are placed at the entrance of the burrow.

- ♦ Worm-like.
- ♦ 2mm-14cm long
- ♦ Lack foot, and shell (spicules in place of a shell).
- ♦ Movement by peristaltic contractions.
- ♦ Mantle covers entire body.
- ♦ Head is poorly developed/reduced (no tentacles, no eyes).
- ♦ They have a radula and style sac.
- ♦ No excretory organs or gonoducts.
- ♦ Some lack radula.
- ♦ Gonochoristic (separate male and female/dioecious).
- ♦ E.g. *Neomenia* sp., *Chaetoderma* sp., etc.

3.3.2 **Neomeniomorpha (**solenogasters; Aplacophora**)**

About 180 species are known. They resemble the chaetodermomorphs in the following features:

- ♦ Worm-like and elongated.
- ♦ They have no shell
- ♦ Essentially headless
- ♦ No radula in some
- ♦ No gonoducts

They differ from the Chaetodermomorpha as follows:

- ♦ 1mm-30cm long
- ♦ Body laterally compressed
- ♦ Ventral groove
- ♦ Greatly reduced foot
- ♦ Mantle covers body; 1 or more layers of calcareous scales are embedded in mantle.
- ♦ No ctenidia/gills
- ♦ Gills in form of papillae or folds may develop secondarily.

- Mantle cavity postero-ventral.
- Movement is by gliding.
- All species are hermaphrodites.
- Copulation occurs with the aid of stylets.

Despite their close resemblance to chaetodermomorphs, neomeniomorphs are considered to be closer to shell-bearing molluscs. It is not clear how they feed since the have no radula. The two classes are sometimes classified together as Aplacophora, meaning no shell.

3.3.3 Class Monoplacophora (single plate)

- They are circular in shape and bilaterally symmetrical.
- They resemble limpets but their shell is tipped forward.
- The shell is made from one unit with definite growth rings.
- The foot is well developed, broad and flat and disc-shaped.
- They have internal metamerism (the only segmented molluscs).
- Their nervous system lacks ganglia
- E.g. *Neopilina*

3.3.4 Class Polyplacophora (bearer of many plates; Chitons; Amphineura)

- Their body is oval, bilaterally symmetrical and dorso-ventrally flattened.
- The foot is flat and occupies most of the ventral surface of the body.
- The mantle forms a thick girdle around the foot.
- The shell is made up of many units (usually 8).
- There are ctenidia in two rows, one on either side of the body.
- The head is reduced without eyes or tentacles.
- Sexes are separate.
- Fertilization is external.
- The trochophore larva develops to adult without passing through the veliger stage.
- E.g. *Chiton*

4.0 Conclusion

Molluscs are soft-bodied, bilaterally symmetrical, unsegmented, triploblastic coelomate invertebrate animals, whose body is divided into a head, ventral muscular foot and a dorsal visceral hump.

5.0 Tutor Marked Assignment

1) What is the fate of the coelom in molluscs?
2) How did the hypothetical ancestral mollusc move?
3) How many classes of molluscs are there? Name them.
4) What is the function of the radula?
5) The body of the mollusc is described as monomeric. Explain.
6) What is the function of the mantle?

6.0 Summary

There are about 100,000 species of molluscs. Morphological studies of molluscs are usually based on the ‘Hypothetical ancestral mollusc’. There are eight recognizable body forms that have resulted in the eight different classes. All molluscs have a mantle which is responsible for the production of the shell. The feeding organ is called the radula which acts as a rasp. Gaseous exchange is through ctenidia/gills. Eggs cleave spirally and development is indirect through trochophore and veliger larval stages.

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<u>FIGURES</u>

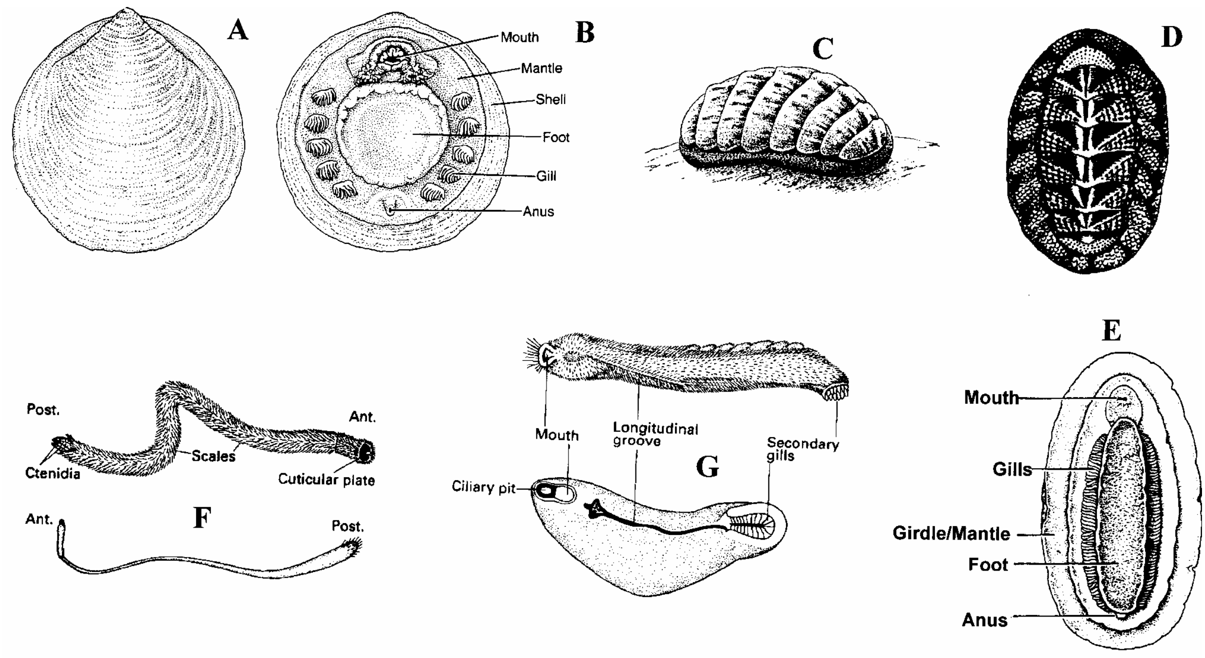

Fig. 5.5. Phylum **Mollusca**, Class **Monoplacophora**: **A,** *Neopilina* (ventro-lateral view), **B** (ventral view). **C, E,** *Chiton* (dorsal and ventral views). (Class **Polyplacophora); D,** another morphological type of Polyplacophora; **F,** Two chaetodermomorphans (Class **Chaetodermomorpha); G,** Two neomeniomorphans (Class **Neomeniomorpha)**. *Sources:* Mitchell *et al.* (undated), Barnes *et al.* (1989); Kershaw (1988).

Study Unit 6: The Phylum Mollusca (Molluscs)

Contents

Study Unit 6

THE PHYLUM MOLLUSCA (MOLLUSCS) *continued*

1.0 Introduction

We introduced the phylum Mollusca in the last study unit. By way of introduction, we looked at the uniqueness of the phylum and pointed out the fact that there was a great deal of variation within the phylum and that the classes bore very little resemblance to each other. We also saw how there were eight morphologically distinct classes within the phylum. In examining the classes, we observed that, in body shape, molluscs ranged from cylindrical, burrow-dwelling 'worms' lacking both a foot and a shell, and greatly elongated along their antero-posterior axes, to almost spherical, effectively headless clams encased within large bivalve shells; while in size they extended from 2 mm long planktonic and inter-tidal species, to the giant squids which measure, including their arms, more than 20m in length, in their case, as a result of elongation in the ancestral dorso-ventral plane. Molluscs occupy all major habitats and include representatives of all known feeding types; they include the most and the least mobile of all free-living invertebrates. Within the same phylum there are also members with some of the least developed brains and sense organs, together with the most intelligent of invertebrates.

We shall place special emphasis on the gastropods and the cephalopods because of the large number of species, economic value and familiarity of the former and several features of biological interest in the latter, as they are said to be similar to vertebrates in several ways.

2.0 Objectives

By the end of the study unit, you should be able to:

- Know the diagnostic features of the scaphopods, bivalves, gastropods and cephalopods.
- Appreciate the deviation of members of the classes from the basic body plan of molluscs
- Relate the morphological features of members of the classes to their lifestyle.
- Appreciate how sophisticated cephalopods are.

3.0 Characteristics of the molluscan classes *contd.*

3.1 Class Scaphopoda (tooth-shells; tusk-shells)

- The body is elongated nearly cylindrical and bilaterally symmetrical.
- The shell is tubular, tusk-shaped and open at both ends.
- They have a short foot.
- They lack a heart.
- The head is reduced with no eyes but has bundles of ciliated prehensile tentacles called **captacula** used for feeding.

Only about 900 species; e.g. *Cadulus* sp., *Dentalium* sp., etc.

3.2 Class Bivalvia (Lamellibranchiata; Pelecypoda; bivalves; clams; oysters; scallops)

The name ‘Bivalvia’ comes from their having two shell valves. There are about 20,000 species of bivalves. They are laterally compressed molluscs completely enclosed within two shell valves. They are relatively sedentary, several being cemented or otherwise attached to the substratum, and; the head is greatly reduced. The missing sense organs of the head may be replaced by tentacles, and in a few, eyes placed around the margins of the mantle. Their very prominent gills are used for filter-feeding as well as respiration.

3.2.1 Characteristics:

- ♦ They are all aquatic and are found in freshwater and the sea.
- ♦ They are bilaterally symmetrical.
- ♦ Their body is laterally compressed and enclosed in a shell that develops as two large plate-like valves hence the name Bivalvia.
- ♦ The head is rudimentary (greatly reduced).
- ♦ They lack tentacles, eyes and radula.
- ♦ The foot is wedge/hatchet/tongue-shaped and can be protruded for ploughing into soft deposits.
- ♦ They are mainly filter feeders.
- ♦ Fertilization is external.
- ♦ A **glochidium** is the final larval stage of somefreshwater bivalves.
- ♦ E.g. *Mytilus* (mussel); *Ostrea* (oyster), *Pecten*, *Anodonta*, *Ensis*, *Teredo,* etc.

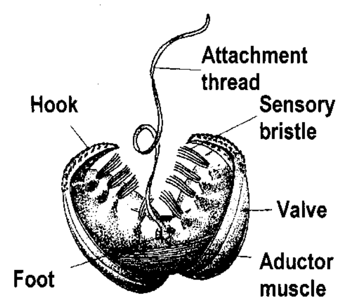

Fig. 6.1. A glochidium of *Anodonta. Source:* Kershaw (1988)

3.3 Class Gastropoda (belly-footed; belly foots)

The name Gastropoda describes a group in which the broad foot occupies most of the underside; The stomach and digestive gland sit on top of the muscular foot. The class Gastropoda is the largest molluscan class with over 75,000 living species, and a long fossil record. Gastropods show considerable adaptive radiation and are found in all types of marine environment, both at the surface and on the bottom, as well as in freshwater and on dry land. Generally, gastropods have a well developed head with tentacles and an asymmetrical body. The visceral mass has been twisted through 180° so that the mantle cavity, ctenidia, anus, and nephridiopores lie immediately behind the head, a modification known as **torsion**. The shell is adapted as a house into which the animal can retreat rather than as a simple protective shield. Considering the wide variety of habitats that the gastropods have invaded, they can be considered as the most successful group of molluscs. Perhaps the most significant features of the gastropod body plan are **torsion** and **coiling**.

3.3.1 Torsion

All gastropods share this phenomenon during their embryonic development (embryology). Torsion is the anti-clockwise rotation of the visceral hump/mass through 180 degrees, bringing the mantle cavity from the posterior to the anterior position. Torsion is caused by the differential growth of the two pedal retractor muscles. The advantage of the anterior position of the mantle cavity might include:

- the provision of accommodation for the well-developed head on retraction of the gastropod into its shell and
- the chemoreceptors (**osphradia**) are brought to the anterior end of the animal so that it can sense the water ahead during movement.

As a result of torsion, the exhalent water current bearing excretory products would pass over the head. The gastropods have overcome the dumping of excretory products over the head by modifying the path of the exhalent current by:

- The development of a slit in the shell by some, through which the exhalent current can leave.
- Secondary detorsion through 90 degrees in some of them, so that the mantle cavity lies on the right side of the body and the anus becomes posterior.

Fig. 6.2. The **veliger larva** of a gastropod: **A**, Before torsion. **B**, After torsion. Note that after torsion, the anus is brought to lie above the mouth. *Source*: Buchsbaum et al. (1987).

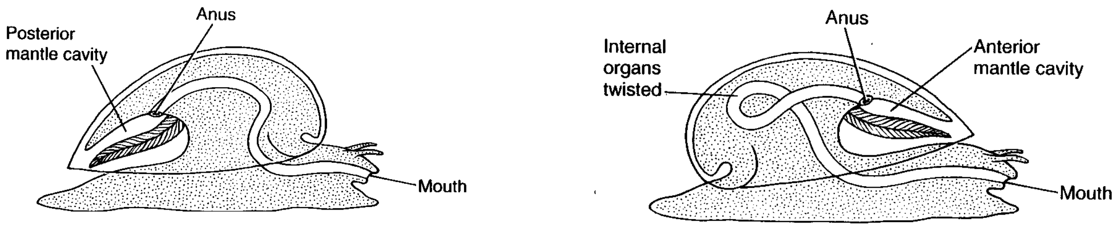

Fig. 6.3. An illustration of the effect of torsion on the body plan of the gastropod. **Left**: Before torsion; **Right**: After torsion. *Source:*

3.3.2 Coiling

Most gastropods are snails with a helically coiled shell and visceral mass. The helical coiling results from unequal/asymmetrical growth. Most snail shells are in the form of a right-handed coil, which leaves less room for organs of the right side; many snails do not have the right gill, the right excretory organ and the right auricle.

The change in the design of the shell involved an increase in height and a decrease in aperture, thereby changing the shell shape from a shield to a cone. This cone-shaped shell must have been cumbersome to carry around and would have made it difficult for the gastropod to search around for food especially in crevices and holes. This problem was overcome by the spiraling of the shell over the head as it became higher and more conical.

The early coiled shell was planospiral i.e. bilaterally symmetrical with each spiral located outside the preceding one, and in the same plane i.e. resembling a coiled hose lying flat on the ground.

The reduction in shell aperture that resulted in the limitation of the space within the margin of the mantle may have accounted for the reduction of the gills, retractor muscles and nephridia to a single pair, which is the maximum number in any gastropod.

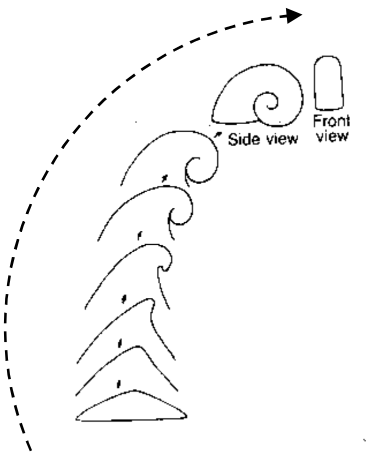

Fig. 6.4. Evolution of the planospiral shell. The height of the shield-like shell of the hypothetical ancestral mollusc increases forming a peak; the peak is pulled forward and coiled under. Aperture is reduced and animal can withdraw into spiral shell, which is more compact and less awkward to carry than a straight conical shell. Note that the shell is bilaterally symmetrical. *Source:* Barnes (1980)

Although there is fossil evidence of the planospiral shell, all living gastropods have the asymmetrical shells or secondarily derived symmetrical shells. The disadvantage of the planospiral shell is that it is not compact and therefore cumbersome. This problem was solved with the evolution of asymmetrical coiling, where the coils were laid down around a collumella with each coil lying beneath the preceding one. This type of shell is relatively compact and may have a globular shape, despite its length.

The new type of shell could not be carried as the old planospiral shell since all the weight would hang on one side of the body. For a fairly even distribution of weight, the shell was shifted so that the axis of the spiral slanted upwards and somewhat posteriorly, resulting in the shell being carried obliquely to the long axis as we have in living gastropods. The change in the symmetry of the shell and its carriage must have happened at the same time.

3.3.3 Other characteristics of the gastropods:

- They are mainly marine but some occur in freshwater and terrestrial habitats.
- Possess distinct and well-developed head bearing tentacles and eyes.
- They have a well-developed radula.
- They have a flat muscular ventral foot used for creeping.
- They may or may not possess a shell and if present, a single unit.
- Fertilization is internal.
- E.g. the giant West African land snail, *Achatina*, *Patella* (limpet), *Limax* (slug), *Haliotis* (abalone), etc.

3.4 Class Cephalopoda (head-footed; nautilids, squids, cuttlefish and octopuses)

The name of the class means 'head-footed', because the foot is closely associated with the head. Like in the gastropods, the shell has been reduced in varying degrees. *Nautilus* is characterized by a large external coiled shell, whereas, the squids have a thin non-calcified cellophane-like vestige of a shell embedded in the mantle; cuttlefishes have a calcified shell that is also reduced and embedded in the mantle; octopuses have no shell at all. The reduction of the shell is correlated with a more active swimming lifestyle; it is a buoyancy device in the cuttlefishes. The nautiloids are poor swimmers with their massive, many-chambered shell. The primary body plan of the class as a whole is one of swimming and predatory existence, although some cephalopods such as the octopus have secondarily assumed a less active bottom-dwelling habit. The features of the squid and cuttlefish illustrate how the molluscan body plan has been so altered as an adaptation to an active swimming life. The head is surrounded by a circle of large prehensile tentacles which are homologous to the foot of other molluscs. Like in the gastropods, the cephalopods are elongated along the dorso-ventral plane, but because of their swimming lifestyle, the ancestrally ventral surface has become the anterior end and the dorsal (visceral hump/mass) has become the posterior end, functionally. Many cephalopod features are directly or indirectly related to their active life and the correspondingly higher metabolic rate. These features include: secondarily folded gills; absence of gill cilia; closed blood circulatory system; accessory branchial hearts; the respiratory pigment haemocyanin; highly developed eyes; complex nervous system and behaviour; chromatophores and ink gland.

3.4.1 Other features/Characteristics

- They are exclusively marine animals
- They are bilaterally symmetrical.
- The long axis of the body is dorso-ventral.
- They are the largest in size and the most advanced group of invertebrates.
- The cephalopods especially squids have evolved many similarities to vertebrates e.g. the squids have an internal cartilaginous support analogous to the vertebrate skeleton; they also have a cartilaginous brain case.
- They have well-developed eyes.
- They have a closed blood circulatory system (blood is confined in vessels).
- The shell may be massive and external, reduced and internal or completely absent.
- The radula is well developed and in addition, there is a pair of horny mandibles that form a beak.
- Development is direct although juveniles of some are planktonic.
- The nervous system is well developed with a large and complex brain.
- E.g. *Octopus, Argonauta, Sepia* (cuttlefish), *Loligo* (squid), *Nautilus* etc.

Cephalopods are now represented by only about 400 species compared with more than 10,000 different fossil forms. There are three subclasses of cephalopods, one fossil and the other two **extant.**

a) **Subclass Ammonoidea.** These are fossil forms with coiled external shells and complex septa and sutures.

b) **Subclass Nautiloidea**: External shells which may be coiled or straight; shell sutures simple; several slender suckerless tentacles; 2 pairs of gills; 2 pairs of nephridia. *Nautilus* is the only surviving member of this group.

c) **Subclass Coleoidea:** Shell internal or absent; few tentacles with suckers; one pair of gills; one pair of nephridia. Five orders: 1 extinct and 4 extant. E.g. *Spirula, Sepia, Idiosepius, Sepiola, Rossia* (Order Sepioidea); Squids: *Loligo* (Order Teuthoidea); *Vampyrotheutis* (Order Vampyromorpha); the octopus: *Argonauta*; *Eledone*, *Eledonella* etc. (Order Octopoda: 8 legs)

4.0 Conclusion

In terms of number of described species, the class Gastropoda is the largest of the mollusc classes; it is also the most widely distributed. The gastropods alone display the phenomena of coiling and torsion. Cephalopods are the most sophisticated of the molluscs and indeed the invertebrates.

5.0 Summary

The shells of scaphopods are tusk-like but tubular and open at both ends; they use captacula for food acquisition. Bivalves are laterally compressed and practically headless; they use their gills for feeding. All molluscs except bivalves have a radula. The gastropods are more numerous than the other molluscs and occupy marine, freshwater and terrestrial habitats. Torsion occurs in gastropods during development, bringing the mantle cavity and anus to the anterior position. Coiling of the shell and visceral mass make the shell less cumbersome than the ancestral type. The cephalopods a highly developed nervous system and elicit rapid responses to stimuli as a result of nerve fibres attached to the mantle. They have a closed circulatory system that provides more efficient blood circulation. Their eyes are quite similar in structure to those of vertebrates.

6.0 Tutor Marked Assignment

1). How many classes are there in the phylum Mollusca? Name them.
2). Name the largest of the classes of molluscs.
3). The cephalopods are said to be the most sophisticated of the molluscs. Give two reasons for this statement.
4). State three features of cephalopods that are associated with their active lifestyle.
5). Discuss the phenomenon of torsion. Is it characteristic of all the molluscs?
6). List the subclasses of the Cephalopoda.

7.0 Further Reading/References

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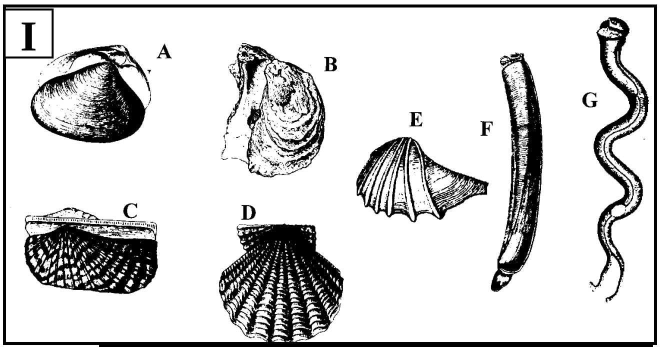
Figures



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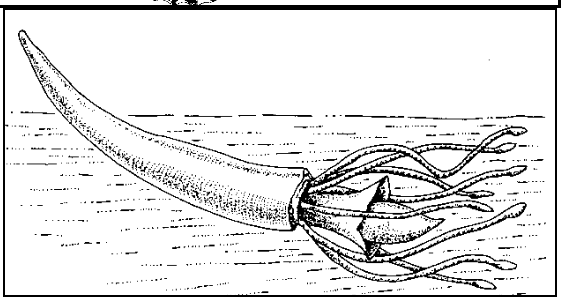

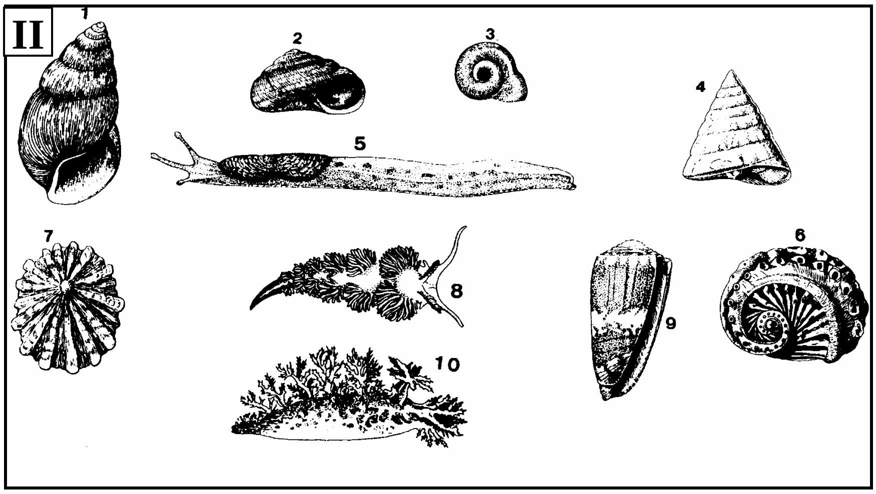

I - Bivalvia: **A,** *Pecten*; **B,** *Ostrea* (oyster); **C**, *Arca*; **D,** *Pecten*; **E**, *Cuspidaria;* ***F,*** *Ensis* (the razor clam); **F,** *Mactra*; **G,** *Teredo* (the shipworm).

II – Gastropoda (shells and species): **1,** *Achatina;* **2,** *Triodopsis;* **3,** *Helisoma;* **4,** *Trochus;* **5,** *Limax;* **6,** *Haliotis* (abalone); **7,** *Acmaea* (a limpet); **8,** *Eolis* (a nudibranch)*;* **9,** *Conus* (Cone shell); **10,** *Dendronotus* (a nudibranch)

III – **Cephalopoda**: **A,** *Nautilus* lateral view; **B**, as it appears when creeping; **C,** *Octopus vulgaris*, resting position; **D,** *Sepia*, a cuttlefish; E, *Loligo*, a common squid; **F,** *Architeuthis*, the giant squid, total length of ♀ = 13m (43 feet); ♂ = 10m (33 feet); it used to be the largest known invertebrate but currently *Mesonychoteuthis hamiltoni* (Colossal squid; Antarctic squid) whose smaller immature specimens measure 12-14m is regarded as the largest invertebrate alive.

IV - Class **Scaphopoda**: *Dentalium* in position with captacula extended for feeding.

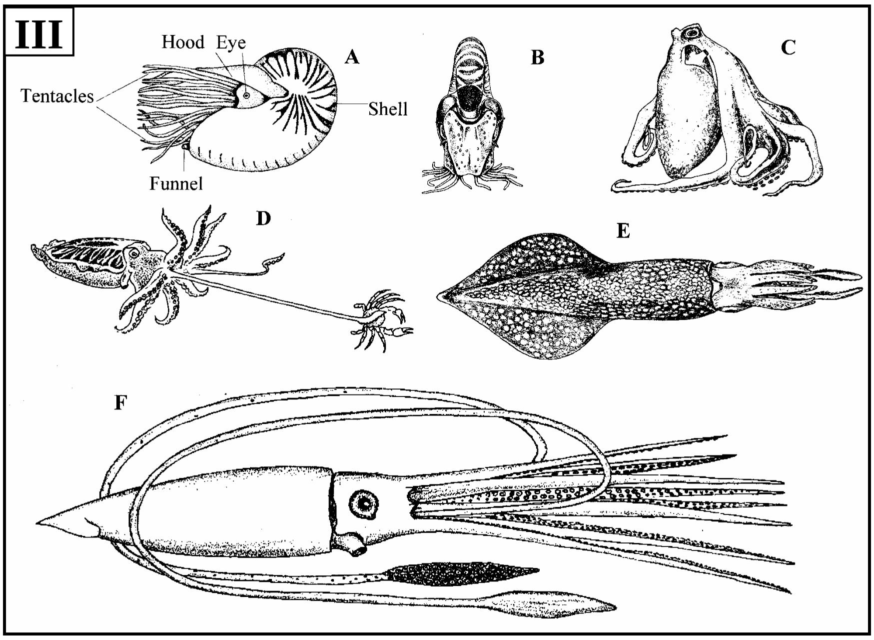

Fig. 6.5. Body forms and shells of some mollusk classes. *Sources:* Meglitsch (1972). Kershaw (1988); Barnes (1980); Barnes *et al.* (1989); Mitchell *et al.* (undated); Hegner & Engermann (1968).

Study Unit 7: Phylum Mollusca (Molluscs) *continued*

Contents

Study Unit 7

THE PHYLUM MOLLUSCA (MOLLUSCS) *continued*

1.0 Introduction

We are now familiar with the diversity of the phylum mollusca, judging from the variety of body form, classification and some aspects of their lifestyle, that were introduced in the last two study units. The molluscs are many and varied but we shall select one of the common ones that depict many of the features that were introduced in the preceding units, for study. In this unit, we shall study some aspects of the organization of a member of the largest and most familiar classes, Gastropoda, as a representative mollusc. The giant African snails, *Achatina achatina* and *A. fulica*, are gastropods; they belong to the same subclass and are anatomically very similar to *Helix pomatia*, which we are studying as a representative of the phylum Mollusca. The pulmonates, of which *Helix* is one, are principally characterized by the conversion of the mantle cavity into an air-breathing lung with a contractile opening, the pneumostome. The majority are grazers of land plants, many pulmonates have retained the spiral gastropod shell, although it is usually thin, but several members of one terrestrial order have lost it and are called land slugs.

2.0 Objectives

By the end of this study unit you should be able to:

- Appreciate the morphology of *Helix*, a representative mollusc.
- Know the body plan and its modifications in gastropods.
- Understand the role played by the shell of molluscs.
- Note the modification of the mantle in terrestrial gastropods.
- Relate the anatomical structures examined to the functions they perform.

3.0 *Helix*

The genus *Helix*, a member of the subclass Pulmonata, is a gastropod which shows molluscan adaptations to a terrestrial mode of life. *Helix pomatia*, the Roman snail, is the largest British pulmonate and has a long history of being eaten by humans. It is believed that the Romans introduced *H. pomatia* to Britain, hence its common name. *Helix pomatia* lives in open woodland, quarries, banks, and hedges on calcareous ground, but not usually on cultivated land such as gardens or parks. *Helix aspersa*, a rather smaller species, is extremely common in gardens and may also be found in quarries, hedges, and banks. It often has a fixed 'home' in a sheltered place to which it returns after each foraging period; these homes may be used by many generations of snail. Both species feed at night and after rain. In Britain they hibernate during the winter. *Helix pomatia* buries itself just below the surface of the soil, while *H. aspersa* congregates in groups in hidden places or may also bury itself. During hibernation the shell aperture is sealed with an operculum which is a membraneous diaphragm of hardened mucus impregnated with calcium carbonate and small quantities of silica, phosphates and iron.

3.1 The shell

Like in all shell-bearing gastropods, the most conspicuous external feature is the shell, which is spirally coiled. The structure, which we discussed earlier under coiling, can be easily understood by regarding it as an elongated, hollow cone, wound round a central hollow axis, the **columella**. The columella opens at a small ventral pore or **umbilicus** and the sutures between the coils are closely fused. The shell gradually grows longer and wider in an increasing spiral shape, to better accommodate the growing animal inside. The animal also thickens the shell as it grows, so that the shell stays proportionately strong for its size. The shell consists of three layers: an outer horny pigmented periostracum of **conchiolin**, a middle calcareous cross-lamellar layer formed of long strips of **aragonite** in a conchiolin matrix and an inner layer of **nacre**. Getting enough calcium for shell formation is a particular problem for terrestrial snails. As a result of this problem, snails are largely restricted to regions where the soil contains a fair amount of calcium. *Helix* is known to store excess calcium carbonate in cells in the digestive gland. When reared on a diet that lacks calcium, the resulting shell is thin and transparent or it may fail to provide complete coverage for the visceral mass/hump.

3.2 The body

When the snail is resting the head and foot are pulled into a large chamber created by the lowest whorl of the shell, by contraction of a columellar muscle. This muscle originates on the columella, runs down the side of the visceral mass, and splits into bundles extending to the head and anterior and posterior foot. In *H. pomatia* the columellar muscle is known to contract to a tenth of its relaxed length.

When the snail is active the head and foot protrude anteriorly and posteriorly respectively, from the aperture of the shell. The foot is very conspicuous, broad and very muscular with a flat undersurface; the head bears two pairs of tentacles and a slit-like mouth. The rest of the soft parts of the body form the visceral hump/mass which is always enclosed by the shell. The lower margin is thickened and fused with the edge of the mantle to form a collar. These last are secreted by the mantle. Fusion of the mantle margin to the head and foot modifies the mantle cavity as an enclosed space, the lung. Air passes into the lung through a conspicuous opening on the right hand side, the pneumostome.

3.3 Locomotion

Locomotion in *Helix* can be compared with that of the gliding movements of large free-living turbellarians (flatworms). The flattened ventral surface (sole) of the foot is pulled into a series of minute ridges by waves of contraction of the pedal musculature. The musculature is a complex web (including dorsoventral, longitudinal, transverse and oblique fibres) whose contraction is controlled through a nerve net by the pedal ganglion (this will be seen when the nervous system is discussed later). The edges of the ridges are directed backwards and waves of contraction pass from the posterior towards the anterior end. About eight waves may pass over the sole in sequence at any one time. As a result the animal is pushed forwards.

For gliding movement of this kind it is necessary for the surface to be lubricated; the necessary lubrication is provided by mucus produced by epidermal glands in the sole as well as by an anterior glandular mass, the pedal gland. After the animal has passed over a surface, the mucus dries, leaving a shiny snail trail.

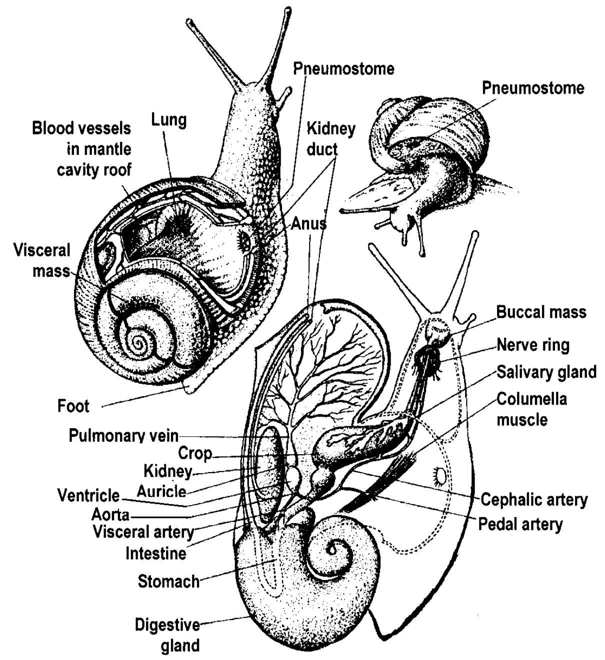

Fig. 7.1. *Helix*: External features and Circulatory, Respiratory and Digestive systems. Source: Kershaw (1988).

3.4 Digestive system and Feeding

Helix is herbivorous and feeds on a wide variety of plants. *Helix aspersa* can damage young plants and soft fruit in gardens. The mouth opens into a buccal cavity with a tongue-like **odontophore** extending from its floor. The odontophore is supported by structures called cartilages, and moved by a complex array of muscles. The odontophore is covered by a thick cuticle; the radula is fused to this cuticle; the whole structure just described is called the buccal mass. The radula consists of chitin and bears a series of highly regular recurved teeth, formed of chitin and hardened protein impregnated with iron and silica.

The buccal mass is protruded through the mouth and the radula is used to tear or scrape off food material. It is withdrawn by a well-developed retractor muscle (the diagram of the operation of the radula was given in unit 5). The radula is continuously worn away through use, and is renewed by specialized cells called **odontoblasts,**

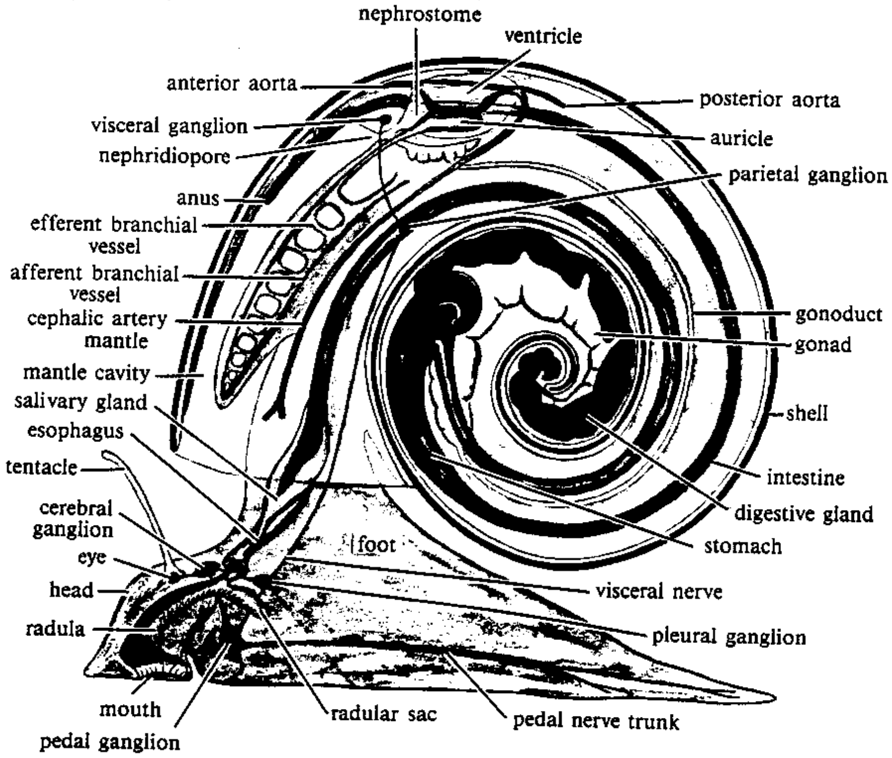

Fig. 7.2. A scheme of gastropod organisation. *Source:* Meglitsch (1972).

which lie at the inner end of the radula sac, into which the posterior end of the radula fits. The floor of the radula sac secretes a ribbon of cuticle onto which the teeth are fused. As more rows of teeth are secreted the entire structure moves forwards until it appears on the dorsal surface of the odontophore.

The particles of food are taken into the buccal cavity which opens at its posterior end into a narrow tubular oesophagus. Two elongated salivary glands, which secrete watery mucus containing amylase and other enzymes, open into the roof of the buccal cavity. This secretion lubricates the moving radula and begins the process of digestion.

The oesophageal wall is thin and muscular with a glandular ciliated lining; it widens posteriorly to form a large thin-walled crop. The cilia beat to give a strong, backwardly-directed current which, by the peristaltic movements of the wall of the oesophagus, force the food towards the crop. Enzymes produced by the oesophageal glands mix with the food. In the crop, further mixing takes place with a brown digestive fluid containing enzymes produced by the digestive gland. In addition to these, symbiotic bacteria living in the crop and intestine are thought to produce a cellulose-splitting enzyme, cystase, which may also be secreted by the digestive gland.

The digestive gland opens into the stomach, which follows the crop. It is a voluminous organ, which is brown in colour and forms packing tissue throughout the visceral hump. In *Helix* it is composed of three kinds of cells: enzyme secreting cells, absorptive cells, and calciferous cells (responsible for calcium carbonate storage). The stomach has a ciliated lining and particles of digested food are swept into the digestive gland for absorption. Indigestible matter is carried to the distal end of the stomach and from there to the coiled intestine. A style and style sac are absent in *Helix* but are both typically present in gastropods. The intestine extends to the rectum which opens, via the anus, into the mantle cavity just behind the **pneumostome**.

From the account given above, *Helix* is herbivorous. Other feeding habits, in other species of gastropods include predation, scavenging and in a few cases, suspension feeding. There are also carnivorous gastropods which also use their radula for their feeding. Some carnivorous gastropods drill through other mollusc shells with their radula and assisted with enzymatic secretion, to access the soft tissues of other molluscs e.g. the oyster drill *Urosalpinx cinerea*.

Cone shells are also carnivores, feeding on other molluscs, annelids and even fish; they have a highly specialised feeding apparatus, instead of having a radular ribbon they have individual radular teeth, like darts. The cone shell (e.g. *Conus striatus*) thrusts its radular tooth into the soft tissues of its victim, while retaining hold of the other end. The victim is very quickly immobilized by the poison which is injected through the hollow cavity of the tooth.

3.5 Gaseous exchange

A major characteristic feature of the pulmonates is the conversion of the mantle cavity into an air-breathing lung. The mantle cavity is modified to form a lung by fusion of the mantle edge to the back and neck in front of the visceral hump. The lung is roofed by the mantle which is extensively supplied with blood by the pulmonary vein. The floor of the lung is formed by the head and foot which, in their relaxed position, arch up into the lung but can be flattened by contraction of intrinsic longitudinal muscles. Gaseous exchange takes place over the surface of the mantle, with air being drawn into the mantle cavity through the pneumostome by alternate arching and flattening of the lung floor. The pneumostome can be closed by a valve, to reduce water loss.

3.6 Circulatory system

In pulmonates such as *Helix*, the heart consists of a single auricle and a ventricle lying within the pericardial cavity. Blood from both the general body surface and the pulmonary vein is received by the auricle and pumped into the ventricle. The single aorta, arising from the ventricle, splits to form a cephalic artery which supplies the anterior part of the body and the foot (as the pedal artery), and a visceral artery which supplies the visceral hump. The arteries branch and enter a series of irregular cephalic, pedal or visceral haemocoelic spaces or sinuses in which the organs lie bathed in blood. The spaces are small and the tissue resembles flatworm parenchyma. Blood is collected by two veins which supply the lung, after which it returns to the heart. The blood contains the copper-based respiratory pigment, **haemocyanin**, which gives it a distinct green colour.

3.7 Excretion and osmoregulation

Helix has a single kidney, representing that of the post-torsion left-hand side. It is a sac of coelomic origin connected to the pericardial cavity by the **renocardial canal** and drained by the kidney duct, or **ureter**, which runs along the rectum to a slit-like opening at the right edge of the pneumostome, close to the anus. Both the renocardial canal and the ureter are ciliated; in the former the cilia beat towards the kidney creating a flow of fluid, although in *Helix* the canal is tiny and the flow of fluid small. The kidney is yellow and has folded glandular walls that secrete uric acid, which can be discharged in solid form, thereby conserving water. Additionally, uric acid can be stored in the kidney over a long period; this is an important factor in survival through periods of hibernation. The greater part of the fluid which enters the kidney through the renocardial canal is reabsorbed.

4.0 Conclusion

Helix is a good representative mollusc as it shows most of the features that have been highlighted for the phylum.

5.0 Summary

The shell of *Helix* shows coiling, which is typical of gastropods. It is produced by the mantle and consists of three layers. The body consists of a well-developed head bearing tentacles, a large ventral muscular foot and a dorsal coiled visceral mass/hump sitting on top of the foot. Helix moves by gliding, which is facilitated by the contraction of muscles and by glandular mucus secretion. It is herbivorous and acquires food by radular scraping and rasping. The digestive gland produces the enzyme for digestion of cellulose. The mantle is heavily vascularized and functions as a lung. Air enters the mantle cavity through the pneumostome. The heart consists of one auricle and one ventricle and the circulatory system is open. The respiratory pigment is haemocyanin and it is green in colour. *Helix* has a single kidney and the excretory product is uric acid, which is solid.

6.0 Tutor Marked Assignment

1). How many layers does the shell of molluscs have? Name them.
2). What is the function of mollusc shells?
3). Which part of the snail produces the shell?
4). How is locomotion over a dry surface facilitated in molluscs?
5). What sort of material does *Helix* feed on?
6). In what part of the body are digestive enzymes produced?
7). Describe very briefly, the process of gaseous exchange in a pulmonate.
8). What benefit do terrestrial gastropods derive from the excretion of uric acid?

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Study Unit 8: Phylum Mollusca (Molluscs) *continued*

Contents

Study Unit 8

THE PHYLUM MOLLUSCA (MOLLUSCS) *continued*

1.0 Introduction

The phylum Mollusca, as we saw in the 5th study unit, is made up of five major morphological types, which included the polyplacophoran, bivalvian, scaphopodan, cephalopodan and gastropodan type of organization, among others, all referable to the 'hypothetical ancestral mollusc'. The examination of the variety of molluscs continued into the 6th study unit, in which we studied the gastropods and the cephalopods in greater depth as a result of some of their fascinating attributes of biological interest. The class Gastropoda, as we have seen, is the largest and most widely distributed of all the mollusc classes. In the 7th study unit that has just been concluded, we started examining the organisation of the Mollusca, using *Helix*, a gastropod, as a point of reference. In the gastropod, we looked at the following aspects of its organization and biology: the shell, the body, locomotion, feeding, gaseous exchange, the circulatory system and circulation, excretion and osmoregulation. In this unit, we are going to continue looking at the organizational biology of the molluscs, using the gastropods, especially the pulmonates, for reference; we shall examine the sense organs and nervous system and the reproductive system and reproduction in the molluscs generally and the terrestrial pulmonates in particular. We shall also look at the economic importance of the molluscs as a group.

Sense organs occur in different parts of the body but more so in the head and foot regions. They include chemoreceptors, light receptors and tactile organs. The nervous system consists of cerebral ganglia, which supply the rest of the body with nerves. Terrestrial gastropods are hermaphroditic; this assures that any two animals that meet can mate, which is especially useful in slow-moving animals. All pulmonates have abandoned larval stages, developing directly into young slugs or snails.

Some molluscs are beneficial to humans while others harm or cause huge economic losses in different ways but most especially by their feeding habits.

2.0 Objectives

By the end of this study unit you should be able to:

- ❑ Know the sensory structures and nervous system of mollusks..
- ❑ Know the structure of the reproductive system of molluscs.
- ❑ Appreciate the benefits that humans derive from molluscs.
- ❑ Appreciate the medical importance of mollusks
- ❑ Know the economic losses caused by molluscs.

3.0 Sense Organs (in gastropods generally)

Tactile (touch-sensing) cells are scattered over the body surface. They are concentrated in regions of high sensitivity, such as the head, the margin of the foot, and sometimes the edge of the mantle. The head tentacles are well supplied with tactile cells, and other tactile projections appear irregularly in different groups. The most outstanding of these are the **epipodial tentacles** (tentacles associated with the feet), found on the sides of the foot of many gastropods and the **cerrata** (projections from the body surface that are characteristic of nudibranchs, also called sea slugs) that occur on the dorsal or lateral surfaces of many nudibranchs (means naked gills) (refer to figures of gastropods in unit 6).

A patch of sensory cells, the **osphradium** (which was mentioned in unit 6 in connection with torsion), occurs at the base of each gill. The osphradium is often a strand of elevated sensory cells associated with the nerve to the ctenidium, but in some cases it is incorporated in the ctenidial axis. Sometimes lateral tracts of elevated cells extend on each side of a central strand. Gastropods without ctenidia retain an osphradium if a mantle cavity and secondary gills are present. Aquatic pulmonates have an osphradium, but **land pulmonates do not**. *Helix* is a land pulmonate and so **does not have osphradia**. Osphradia lie in the path of inhalant respiratory currents. They are chemoreceptors (as we saw earlier). It has been suggested that they may be sensitive to sediment. There is evidence that they participate in chemoreception generally. Chemoreceptors are important mediators of gastropod behavior; this has been established by experimentation. Oriented responses to food are usually well developed in gastropods. It has been demonstrated that some species are unable to detect food and feed normally if the osphradia are removed. The **oral tentacles** of nudibranchs prove to be more important in contact chemoreception involved in feeding. The anterior margin of the foot is also an important site of chemoreception in many aquatic gastropods. Hollow **statocysts** (structures concerned with sense of gravity) containing calcareous particles are almost universally present in gastropods. They receive nerves from the cerebral ganglia. Statocysts do not occur in sessile gastropods. Generally, creeping gastropods have statocysts in the foot. Most gastropods have **eyes** at the base of the head tentacles. Some slug-like marine pulmonates have **mantle eyes**, located on tubercles on the dorsal surface.

3.1 The nervous system

In *Helix*, the ganglia, **commissures** (connecting bands of nervous tissue) and **connectives** (connecting band of nerve fibres between two ganglia) characteristic of molluscs are concentrated near the anterior end to form a nerve ring enclosed in a connective tissue envelope around the oesophagus and salivary ducts. Nevertheless some distinctions can be made between the component structures of this ring. The cerebral ganglia lie dorsally and are linked by a pair of cerebro-buccal connectives to the small buccal ganglia which lie lateral to the salivary gland ducts. The cerebral ganglia give off nerves to the body wall, mouth tentacles and eyes, and the buccal ganglia supply nerves to the buccal mass and cavity. Paired **cerebro-pedal** and **cerebro-pleural** connectives extend ventrally from the cerebral ganglia to the pedal and pleural ganglia respectively. The latter are joined by fused visceral ganglia to form a ring through which the cephalic artery passes. The ganglia supply nerves to the various body organs and the foot. The structure of the nervous system is easier to describe as if torsion had not occurred (Fig. 8.1).

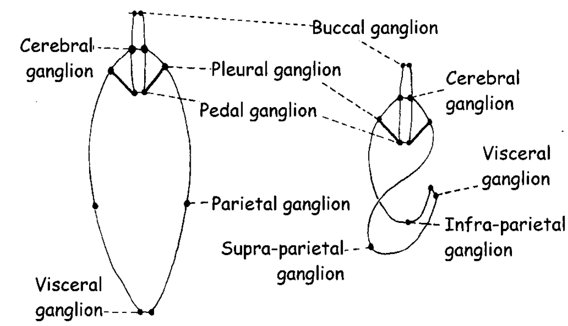

Fig. 8.1. A, Hypothetical pre-torsion nervous system; **B,** Post-torsion nervous system. *Source:* Barnes (1980)

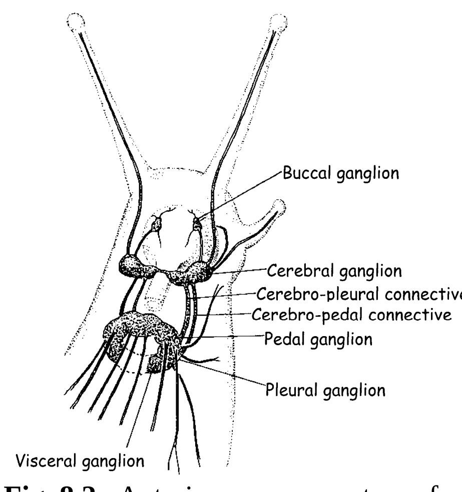

Fig. 8.2. Anterior nervous system of *Helix*. *Source:* Kershaw (1988).

3.2 The Reproductive system and reproduction

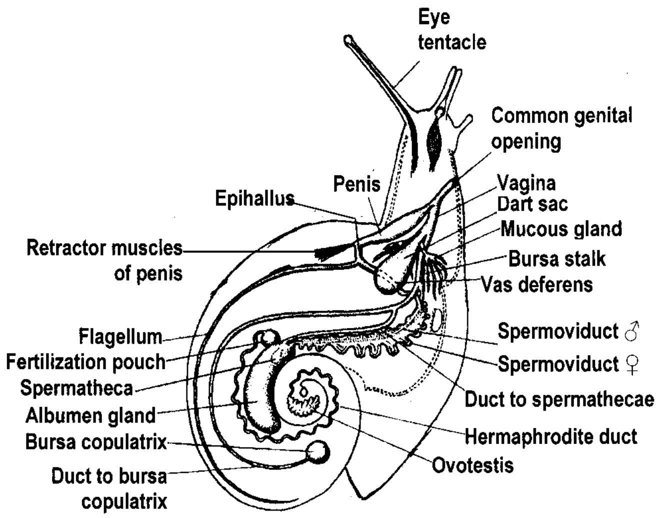

Fig. 8.3. The reproductive system of *Helix*

Helix is hermaphrodite. Copulation takes place accompanied by mutual exchange of sperm in the form of **spermatophores**, and fertilization is internal (a common adaptation of terrestrial animals). A single gonad (the **ovotestis**) produces both eggs and sperm simultaneously; it is a small white structure embedded in the digestive gland. Sperm are produced continuously and passed from the ovotestis into a short coiled **hermaphrodite duct** which extends towards the albumen gland. This duct is used as a seminal vesicle and appears to be full of sperm throughout the year. Just before it reaches the albumen gland the hermaphrodite duct dilates forming a fertilization pouch which is connected to the albumen gland chamber by a narrow duct; the pouch also receives short narrow ducts from between three and five sacs called spermathecae, in which sperm transferred from another snail during copulation (foreign sperm) is stored. The albumen chamber is joined to the remainder of the reproductive system by a **spermoviduct** which, as its name implies, is used for transfer of both sperm and eggs and is functionally separated into two grooves by paired longitudinal folds. The wall of the albumen chamber is also deeply folded with one fold forming a groove which joins the fertilization pouch to the sperm groove of the spermoviduct. At the beginning of copulation sperm pass from the hermaphrodite duct through the albumen chamber to the sperm groove, then to the **vas deferens** and **epihallus** where the spermatophore is formed. This process is extremely rapid (taking less than one minute) due to the beating of long cilia which line the entire sperm duct. The spermatophore is an elongated structure with distinct head, neck, body and tail regions; sperm is stored in its body. In *Helix aspersa* (but not in *H. pomatia)* the spermatophore tail is formed in a long caecum or 'flagellum' which extends from the epiphallus. In *H. pomatia* mating occurs immediately after hibernation in Britain, in April or May and possibly also in the late summer. *Helix aspersa* mates throughout the summer. In either case copulation is preceded by an elaborate courtship in which the partners circle round each other, make tentacular contact and entwine their bodies. In *H. pomatia* this phase may last for as long as one and a half days. When the animals are intertwined, a dart sac (part of the vagina) secretes a calcareous spicule which is driven into the partner's body wall and which stimulates copulation. The **intromittent** organ or penis is everted and inserted into the bursa stalk (a direct continuation of the vagina) of the partner. After the spermatophore head has been placed in position, the penis is withdrawn and the rest of the spermatophore is pushed out by the donor and drawn in by the recipient. Partners transfer their spermatophores simultaneously and the whole process is long and slow, taking several hours. Sperm are released from the spermatophore and migrate to the spermathecae. The remains of the spermatophore and any excess sperm are transported along an elongated duct by peristalsis to the bursa copulatrix where they are digested. The snails then -resume their normal activities. Eggs pass down the hermaphrodite duct and are fertilized in the fertilization chamber by foreign sperm transferred from the spermathecae. The eggs are large and yolky; after fertilization they are surrounded by albumen secreted by the glandular lining of the fertilization chamber, and by a leathery calcareous shell as they pass down the oviduct.

Helix lays its eggs in humid places in hollows which it digs with its foot. A typical clutch size is between 19 and 96 eggs. The larval stages develop inside the shell of the egg which enlarges as the developing *Helix* grows. The **veliger** is modified from its basic planktonic form by the development of a large cephalic vesicle in the velar region which provides an increased surface for gaseous exchange. Miniature adult snails emerge from the eggs at hatching. The young snails are complete apart from their reproductive system. Maturation is normally reached in the second year, and mature snails live for several years.

Helix has high regenerative powers, particularly of its shell, although almost any part of the body except the central nervous system can be regenerated if damaged.

3.3 Importance of molluscs to humans

- Bivalves such as clams and mussels, have been an important food source for many different people around the world; this has sometimes resulted in over exploitation.
- Other molluscs commonly eaten include octopuses and squids, whelks, oysters, and scallops. In 2005, China accounted for 80% of the global mollusc catch, netting almost 11 million tonnes. Within Europe, France remained the industry leader.
- The gastropods *Achatina fulica Achatina achatina* and *Tympanotonus fuscatus* are also used as food in different parts of Africa.
- Muscle is used as bait for fishing.
- Lime is manufactured from cuttlebone of cuttlefish (cephalopod) and incorporated into feeds as calcium source.
- Ink from cephalopod ink sac is used as dye.
- Squid beaks are undergoing extreme scientific analysis to assist in the development of replacement knees and hips for humans. The beak is made of a blend of protein, complex carbohydrates and water.
- Research at the University of Otago in New Zealand has shown that jelly produced from squid pen can be used in wound healing.
- Most molluscs that have shells can produce pearls, but only the pearls of bivalves and some gastropods whose shells are lined with nacre are valuable.
- The best natural pearls are produced by the pearl oysters *Pinctada margaritifera* and *Pinctada mertensi*, which live in the tropical and sub-tropical waters of the Pacific Ocean. Natural pearls form when a small foreign object gets stuck between the mantle and shell.
- One method of culturing pearls uses grains of ground shell from freshwater mussels, and over-harvesting for this purpose has endangered several freshwater mussel species in the southeastern USA.
- The pearl industry is so important in some areas that significant sums of money are spent on monitoring the health of farmed molluscs.
- The oyster drill can cause heavy losses in oyster beds.
- A luxury and high-status product made from molluscs is Tyrian purple, made from the ink glands of murex shells.
- Buttons are mode from mollusc shells.
- Sea silk is a fine, rare and valuable fabric produced from the long silky threads (byssus) secreted by several bivalve molluscs, particularly *Pinna nobilis*, to attach themselves to the sea bed.
- Shells of scaphopods (tusk shells) and cowries are used for making jewelry.

- Cowries (especially *Cypraea moneta*) were used for centuries as a currency in Africa. The Ghanaian unit of currency known as the cedi was named after cowries.
- The blue-ringed octopus (*Hapalochlaena*), which is found around Australia, bites when it is severely provoked and its venom kills about 25% of its human victims.
- Another tropical species, *Octopus apollyon*, causes severe inflammation that can last for over a month even if treated correctly.
- The larger species of cone snail that can capture and kill fish are likely to be seriously dangerous to humans. Painful stings and fatalities in humans have been reported.
- The effects of individual cone shell toxins on victims' nervous systems are so precise that they are useful tools for research in neurology, and the small size of their molecules makes it easy to synthesize them.
- Some gastropod species are intermediate hosts to causative agents of some important diseases such as schistosomiasis (bilharzia), which affects up to 200 million people in 74 countries globally and 50% of this number in Africa alone. The disease is debilitating; penetration of the cercariae into human skin causes lesions.
- Some species of molluscs, particularly certain snails and slugs, can be serious crop pests; snails or slugs introduced into new environments can imbalance in the local ecosystems. One example is the giant African snail *Achatina fulica*, which was introduced to parts of Asia and many islands in the Indian and Pacific Oceans, it spread to the West Indies in the 1990s. The predatory snail *Euglandina rosea* was introduced to control it but this was a disaster as the predator ignored *Achatina fulica* and attacked and destroyed several native snail species.
- The glochidia larvae of bivalve molluscs are parasitic on fish.
- The bivalve *Teredo navalis* (shipworm) is greatly elongated with shell valves that have ridged and roughened surfaces for rasping wood by forward and backward rotation. It feeds on the wood particles so obtained. Shipworms do millions of dollars damage to submerged wooden structures around wharfs, driftwood, pilings, and boats by their feeding method. Their digestive gland is specialized for digestion of wood; symbiotic bacteria assist in the digestion of ingested wood.

This list is by no means exhaustive; there may be many more ways in which molluscs impact on humans, directly or indirectly.

4.0 Conclusion

Various sense organs occur in molluscs and the nervous system is well-developed. *Helix* is a hermaphrodite but cross fertilization is the rule. Molluscs are both beneficial and harmful to humans.

5.0 Summary

The sense organs of gastropods include tentacles, osphradia, eyes and statocysts. Pulmonates are hermaphroditic with copulation and mutual sperm transfer. Eggs are deposited within envelopes and development is direct, except in the few marine species. Molluscs impact on humans in various ways: food, ornaments, commerce, medicine and research.

6.0 Tutor Marked Assignment

1). What are osphradia? Do they occur in all molluscs?
2). What is the function of statocysts?
3). Make a good clearly labelled drawing of the anterior portion the nervous system of *Helix*.
4). Discuss what happens after copulation and fertilization in *Helix*.
5). List five ways in which humans benefit from molluscs.
6). List two ways in which humans are harmed by the activities of molluscs.

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Module 2: Coelomate Invertebrates II

Study Unit 1: The Phylum Arthropoda (Arthropods)

Contents

Study Unit 1

THE PHYLUM ARTHROPODA (ARTHROPODS)

Greek: *arthron*, joint and *podos,* foot; these together mean "jointed feet"

1.0 Introduction

About 75-80% of all known animals are arthropods; they constitute the largest phylum in the animal kingdom (estimated at well over one million extant species). Despite their numbers, their total biomass is less than would have been expected due to their relatively small size. The most familiar forms around us are the insects, spiders and crustaceans. Many of the first complex fossilized animals were arthropods and, if their rapid adaptations to changing environments are any indication, arthropods will probably be the last living animals on Earth. Arthropods have exploited every known environment; they are found at all depths in marine, brackish, and fresh waters. They are common in hot springs, saline lakes, temporary ponds, and underground rivers. On dry land they are found in deserts, forests, grasslands and tundra. Their success as terrestrial animals probably owes a lot to their water-conserving excretory system, gaseous exchange organs and desiccation-resistant impermeable cuticle. Many of the species are adapted to a parasitic mode of life. It can be said that, of all animals except humans, the arthropods have made the greatest impact on the Earth's biosphere.

Arthropods have segmented bodies with two or more distinct regions called **tagma**. The body is covered by a tough, sometimes flexible, **chitinous exoskeleton** that serves for both protection and the attachment of muscles and other soft tissues. This covering is a simple device that may explain part of the amazing success of the group. It can be reinforced with minerals to enhance its protective function and still maintain sufficient articulating ability. It is the basis for a variety of arthropod features, from claws and antennae to wings. In terrestrial arthropods, it is an excellent barrier to dehydration. The body plan has a small anterior region (**acron**) and an equivalent posterior region (**telson**) without legs, and a number of intervening sections (segments) each with a pair of legs and serial repeatition of leg-based organs (muscular, nervous, skeletal, etc.). Organs that are not associated with the leg are not serially repeated i.e. the excretory and reproductive systems.

Being covered by an external cuticular system imposes constraints on growth and necessitates a series of moults or ecdysis. This is particularly problematic in arthropods in which the cuticle is also the skeleton. The animal is particularly vulnerable at this time and must be in hiding during the process. The discarded casts were often preserved as fossils.

The Phylum Arthropoda is the third group of coelomate invertebrates we are studying in this course. In this study unit, we are going to look at the characteristics of arthropods and a summary of the different groups it contains.

2.0 Objectives:

By the end of this study unit you should be able to:

- Appreciate the structure and function of the chitinous exoskeleton of arthropods.
- List the characteristic features of the arthropods.
- Recognise common arthropods by their attributes.
- Distinguish arthropods from other invertebrates.

3.0 The Exoskeleton of arthropods

The main distinguishing feature of arthropods, immediately visible to the casual observer, is a tough, semi-rigid cuticular exoskeleton secreted by the epidermis and consisting basically of chitin, a polysaccharide, enmeshed with the protein **arthropodin**. The cuticle is a layered structure, with a thin, non-wettable outer surface. Although the cuticle is always built on a foundation of chitin, this may be invaded or overlaid by different materials in the various arthropod groups, as we mentioned in the 'Introduction'. In insects, the cuticle is rather thin and light but is impregnated with tanned proteins that give it strength and made waterproof by an outer layer of wax. In forms like crabs the cuticle is thick and hard due to the deposition of calcium salts in the **endocuticle**; a degree of water-proofing is provided by lipids in the outer **epicuticle**, and the whole structure is protected by an outer layer of cement.

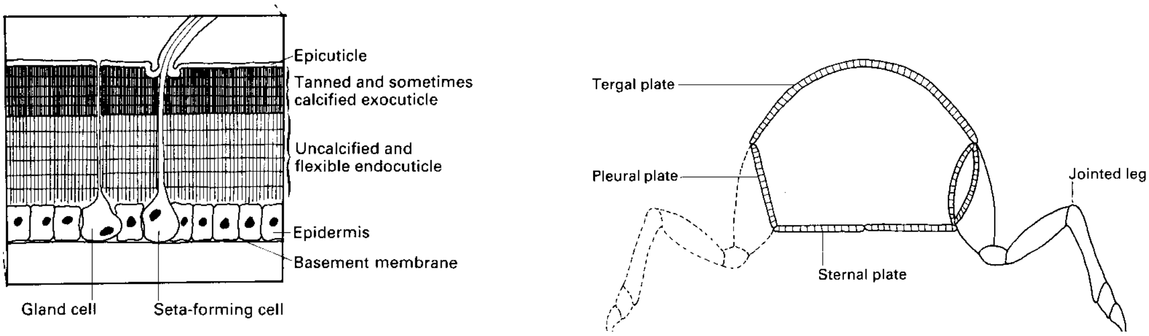


Fig. 9.1. Diagrammatic section through the Arthropod integument (**Left**); Transverse section through the body of an arthropod showing the various exoskeletal plates encircling the body and a jointed limb (**Right**). *Source*: Barnes *et al*. (1989).

3.1 Classification and Characteristics of the Arthropoda

The classification of the arthropods and their evolutionary development and history (phylogeny) has always been controversial but we are not going to examine the controversies here. There are a number of schemes of classification for the arthropods, we are going to select one of them and adhere to it. For the purpose of this course, we shall concentrate on the features of the different groups no matter what name or rank is applied to them. The features will show us how arthropods have been grouped together or separated from others on the basis of their similarities and differences, respectively. Different ranks have been applied to the Arthropoda and its groups but we shall consider it here as a phylum, and its major subgroups as subphyla. Some classifications refer to Arthropoda as Superphylum and its major subgroups as Phyla (sin. Phylum). Some of the characteristics of the invertebrates have been highlighted and briefly discussed in the introduction section of this unit. Other outstanding characteristics of the Phylum Arthropoda are as follows:

- They are bilaterally symmetrical, segmented protostomes, primitively equipped with a pair of appendages attached to each body segment. The appendages are however often reduced or lost in some of the body segments.
- Although all of the post-oral appendages were similar in primitive forms, modern arthropods have appendages that have been specialized for specific functions. Much of arthropod evolution is reflected in the specialization of the appendages, and the nature of the appendages is an important factor in classification.
- The surface of the body and the appendages is covered by a continuous cuticle of complex structure. In most cases the cuticle forms a series of heavy, skeletal plates or rings, connected by thinner, flexible **articular membranes**, permitting freedom of movement.
- Heavy cuticle extends inwards to provide spines or shelves for muscle attachment; these extensions are called **apodemes**.

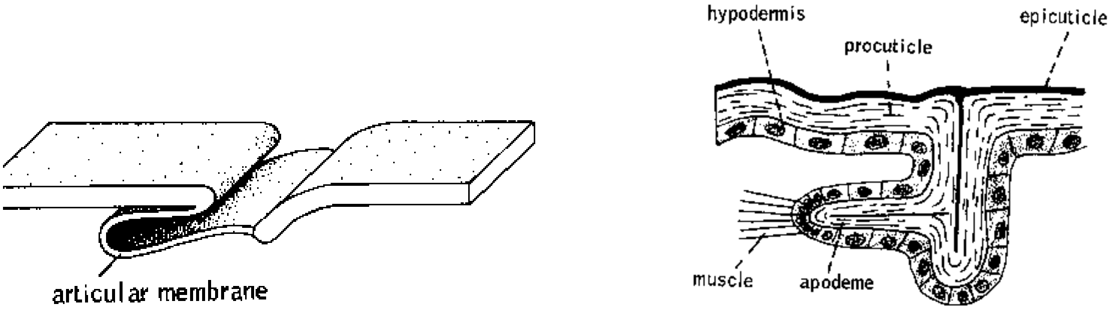


Fig. 9.2. Diagrams showing **articular membrane (left)** and **apodeme** (right). *Source:* Barnes (1980)

- The cuticle forms chitinous linings of the foregut and hindgut. These linings are molted with the surface cuticle during growth.
- Paired, segmental, **coelomic compartments** appear during development, but are greatly reduced with the development of the **haemocoel**; they have an open vascular system.
- A contractile heart, derived from a dorsal blood vessel, lies in a dorsal pericardial sinus. Blood enters the heart through pairs of apertures known as **ostia** (sin. ostium).

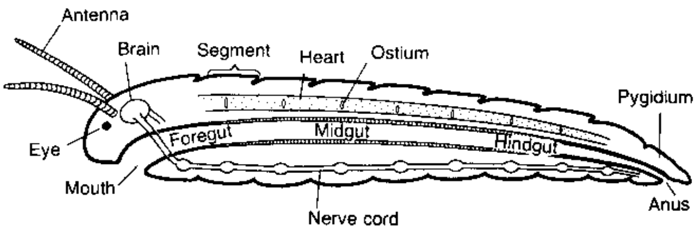


Fig. 9.3. Schematic diagram of the longitudinal section of an arthropod; note the **ostium**. *Source:* Barnes (1980).

- The metameric nephridial system typical of annelids has disappeared with the coelom, although some arthropods have retained some modified nephridia as excretory organs, and the gonoducts may be considered as highly modified nephridia.
- The nervous system is built on the annelid plan, with a double nerve trunk and primitively with segmental ganglia. The brain, however, is more highly differentiated.
- Cilia are completely absent and all movements of the organism or its body parts are dependent upon muscle. With the appearance of an exoskeleton to which muscles can be attached, the muscular system becomes very complex.
- The eggs are richly supplied with yolk, and few show traces of spiral cleavage or a mesoderm stem cell.
- They have different types of larvae but never a trochophore.
- They possess more than one pre-oral segment; they typically have three.
- The cuticle is flexible at some points on the trunk and limbs to provide joints.
- Possess paired jointed appendages on some or all the body segments. Appendages are structures joined to the main body and limbs e.g. mouthparts, antennae, wings, styles, cerci etc.
- Muscles are in discrete bundles.
- They possess compound eyes.
- Their sexes are almost always separate.
- E.g. crayfishes, crabs, spiders, ticks, scorpions, mites, millipedes etc.

Arthropods are said to have evolved from annelids, with which they show certain similarities.

Both groups show metameric segmentation, the segments of arthropods bearing appendages which may be compared with the parapodia of polychaetes. However, in many arthropods the basic metameric pattern in which every segment performs every function is considerably obscured: groups of segments are specialized to perform functions for the entire animal. These groups are known as **tagmata** (singular, tagma) and the whole process is **tagmatization**. Some degree of tagmatization is found in all annelids, but it occurs to a far greater extent in the arthropods and is an important evolutionary trend. One of the advantages of metamerism is the opportunity it provides for specialization of this kind. Other points of similarity between annelids and arthropods include the structure of the central nervous system, and to some extent the arrangement of the circulatory system. Arthropods have a dorsal tubular heart, which may be compared with the annelid contractile dorsal blood vessel. Paired segmental **coelomic compartments** develop in the young arthropod but are greatly reduced in the adult by the development of a blood-filled space, the **haemocoel** (body cavity formed by blood sinuses, often derived from the blastocoel) as the major body cavity.

The Phylum Arthropoda may be classified, based on their diversity of appendages, lifestyles, and other features, as shown in Table 9.1.

Table 9.1. Subphyla and classes of the phylum Arthropoda

Subphylum	**Classe(s)**		
Trilobitomorpha (primitive arthropods)			
Chelicerata	• Merostomata	• Arachnida	• Pycnogonida
Crustacea	• Cephalocarida	• Branchiopoda	• Ostracoda
	• Mystacocarida	• Copepoda	• Branchiura
	• Cirripedia	• Malacostraca	• Remipedia
Uniramia	• Insecta	• Chilopoda	• Diplopoda
	• Symphyla	• Pauropoda	

3.1.1 Subphylum Trilobitomorpha primitive arthropods); Trlobites.

- An extinct group of arthropods now represented by fossils in which the body was molded longitudinally into three lobes, hence the name Trilobitomorpha.
- They had a pair of antennae and all the appendages on the post-antennal somites were of a common type.
- They were marine arthropods and were very numerous in the Cambrian and Silurian but became extinct by the secondary period.
- E.g. *Olenus*, etc.

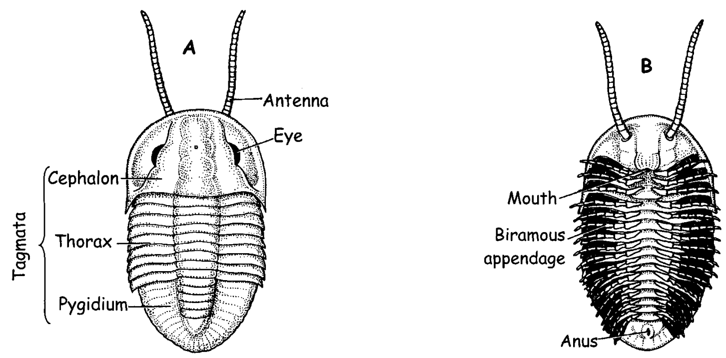
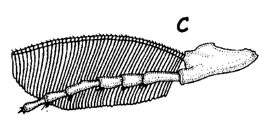


Fig. 9.4. Dorsal (**A**) and ventral (**B**) views of a Trilobite. Note the biramous appendage (**C**) with attached gill. *Source:* Mitchell *et al.* (undated) - Modified



3.1.2 Subphylum Chelicerata

(Greek: *chele*, talon; *cerata*, horns)

There are about 63,000 described species of Chelicerata. The subphylum represents one of the major arthropod evolutionary lines and it includes the well-known spiders, scorpions and ticks. The chelicerates have no antennae and the first pair of appendages (chelicerae), are used in feeding; the name of the subphylum is derived from the chelicerae. The body is divided into two main regions, the **prosoma**, made up of the head and thorax (sometimes referred to as the cephalothorax), and the **opisthosoma**, which is the abdomen.

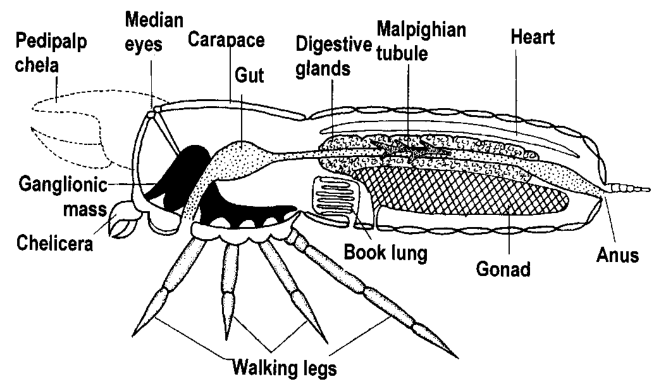


Fig. 9.5. Diagrammatic longitudinal section through a generalised chelicerate. *Source:* Barnes *et al.* (1989).

The characteristics and special features of the Chelicerata are as follows:

1. Bilaterally symmetrical, less than 1 mm-60 cm long arthropods varying in body shape from elongate to almost spherical.
2. They are triploblastic, with tissues and organs.
3. A through, straight gut, from the mid-gut region of which issue from two to many pairs of digestive diverticula (branches), which secrete enzymes and intracellularly digest and absorb food; mouth is anteroventral.
4. Body divided into two regions, an anterior **'prosoma'** formed by the **acron** and six appendage-bearing segments, and wholly or partly covered by a dorsal carapace, and a posterior **'opisthosoma'** without legs and with only highly modified appendages, if any.
5. Appendages uniramous; prosomal appendages comprising one pair of chelate, subchelate or styletlike **'chelicerae'**, one pair of chelate, leg-like or feeler-like **'pedipalps'**, and four pairs of walking legs, all attached near to the ventral mid-line and, in some, extended by haemocoelic pressure; without antennae or jaws.
6. Only one pair of appendages (the chelicerae) form mouthparts, although medially directed processes of the basal article of one or more other limbs ('coxal endites') may crush food or spoon it into the mouth.
7. Usually (unless secondarily lacking) with direct median and indirect lateral ocelli on the prosoma; in one group aggregations of the lateral ocelli form compound eyes.
8. Opisthosoma sometimes externally segmented and then with up to twelve segments, in some divided into a broad anterior **'mesosoma'** and a narrow posterior **'metasoma'**, and in several with a projecting post-anal spine, sting or flagellum.
9. A prosomal excretory system of blind-ending coxal glands, and/or an opisthosomal system of branched endodermal Malpighian tubules arising from the mid-gut and discharging mainly guanine.
10. A non-calcareous exoskeleton and sometimes also with a plate-like mesodermal endoskeleton in the prosoma.
11. Gaseous-exchange organs associated with the opisthosomal appendages or with their embryological primordia; these are external **gill-books** in marine forms and in terrestrial forms, the internal **lung-books** and the sieve- or tube-tracheae derived from them.
12. Blood system involved in the circulation of respiratory gases and usually containing

haemocyanin.
13. Nervous system with separate ganglia along the length of the body or, more usually, concentrated into a single prosomal mass.
14. **Gonochoristic** (dioecious), with external fertilization in solely marine classes (although the two partners associate closely in pseudocopulation during mating) and internal fertilization via copulation or spermatophores in the primarily terrestrial class; gonopores are on the second opisthosomal segment.
15. Juvenile stages small versions of the adult, usually hatching with the full complement of limbs.
16. Originally benthic marine, one class has colonized the land and freshwater very successfully.

NB. Members of the class Pycnogonida differ from the other chelicerates in many respects, and in many of the features listed above.

The subphylum Chelicerata has three classes: Merostomata, Arachnida and Pycnogonida, as shown in Table 9.1. The distinguishing features of the three classes will be highlighted briefly in the next study unit.

4.0 Conclusion

Arthropods are bilaterally symmetrical, coelomate invertebrates with jointed appendages and tough chitinous exoskeleton.

5.0 Summary

About 75% of all named species in the world are arthropods. Arthropods have jointed appendages. They have an exoskeleton of chitin. The exoskeleton provides a surface for muscle attachment. There are four subphyla, Trilobitomorpha, Chelicerata, Crustacea and Uniramia, of which the first is extinct.

6.0 Tutor Marked Assignment

1) What sort of animals are arthropods?
2) Name the type of circulatory system found in arthropods.
3) Name the arthropod classes.
4) Name the major body cavity of arthropods.
5) What is tagmatization.

7.0 References/Further Reading

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Module 2: Coelomate Invertebrates II

Study Unit 2: The Phylum Arthropoda (Arthropods) *continued*

Contents

Study Unit 2

THE PHYLUM ARTHROPODA (ARTHROPODS) *continued*

1.0 Introduction

In the last unit, we introduced the arthropods. We saw how the group consisted of up to 80% of all living species, in terms of their numbers and not their biomass. We stressed the fact that the phylum Arthropoda contained some of the most successful animals, as a result of some of their attributes, one of them being the possession of a chitinous water proof exoskeleton, which is immediately apparent on examining them. We commented on some problems associated with their classification and proceeded to examine their major groups. We noted and commented on the subphylum Trilobitomorpha, a primitive extinct group which is an ancestor to the arthropods, and listed the diagnostic and special features of the subphylum Chelicerata. In this unit, we shall very briefly summarise the distinguishing characteristics of the three classes of the Chelicerata: Merostomata, Arachnida and Pycnogonida, before going on to the third subphylum of the arthropods, Crustacea. We shall examine the structure of the crustaceans and also some aspects of the organisation and biology of *Astacus*, which belongs to the crustacean class, Malacostraca. Our choice is based on its simplicity and manageable size.

The crustaceans are said to be the third largest of the Arthropod subphyla, however in terms of diversity of form they exceed both the insects and the arachnids put together. This great flexibility of structure, along with the general success of the Arthropod body plan (exoskeleton and jointed limbs) has enabled them to be extremely successful as a group. This diversity of form has also made it quite difficult to describe a typical crustacean body plan.

2.0 Objectives

By the end of this study unit you should be able to:

- Appreciate the basic differences between the three chelicerate classes.
- List the characteristic and special features of the crustaceans.
- Describe the body plan of a generalized crustacean.
- Recognise crustaceans by their morphology.

3.0 Subphylum Chelicerata

In the last study unit, we learnt that there were three classes in the subphylum Chelicerata. Brief description of the three classes are given below.

3.1 Classes

3.1.1 Class Merostomata **(horseshoe crabs)**

Horseshoe crabs are not related to "true" crabs at all. There are only 4 living species of horseshoe crabs living in the world's oceans, and they have not changed much in form in the last 350-400 million years. They are now found only in the waters off eastern North America, Southeast Asia, and Indonesia.

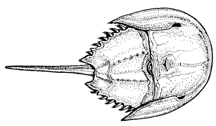
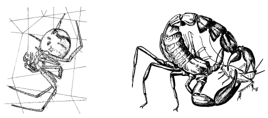
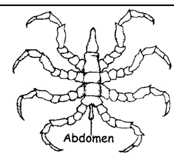
3.1.2 Class Pycnogonida **(sea spiders)**

Although commonly called sea spiders, they are not related to the arachnids, but like arachnids, many of them have 4 pairs of long walking legs. All species are marine, with a fossil record extending back about 500 million years. They are often parasitic on jellyfish, corals, and their relatives, as young, and predators of slow-moving animals as adults.

3.1.3 Class Arachnida (**spiders, ticks, mites, scorpions**)

Arachnids all share a distinctive body plan that unites them and separates them from the other two groups of chelicerates (see the table below). There are about 11 orders of arachnids alive today, containing about 74,000 described species.

Table 10.1. Distinguishing features of the three chelicerate classes (*Source of table*: Meglitsch (1967); *Sources of figures:* Mitchell *et al*. (andated); Barnes (1980) Barnes *et al.* (1989).

	MEROSTOMATA	**ARACHNIDA**	**PYCNOGONIDA**
Prosoma	Continuous dorsal carapace	Single or double carapace	Large, jointed prosoma
Prosomal appendages	Chelicerae and five or six pairs of moderately modified appendages	Chelicerae, pedipalps or legs, four pairs of walking legs	Chelicerae, pedipalps, ovigerous legs, and 4 to 6 pairs of walking legs.
Opisthosoma	12-18 somites plus a telson	11-13 somites, with an additional telson in some	Greatly reduced
Opisthosomal appendages	genital operculum and appendages modified as book gills	vestiges associated with book lungs; special sensory appendages; spinnerets	None
Example(s):	 Horse shoe crab, *Limulus*	 spiders, scorpions, etc.	 Sea spider

3.2 Subphylum Crustacea (crabs, prawns, shrimps, lobsters)

The crustaceans can be regarded as highly successful arthropods, and include shrimps, lobsters and crabs, which are of gastronomic interest, as well as numerous smaller forms. The majority of crustaceans are marine species; about 97% of all marine arthropods are crustaceans, but some live in freshwater; they dominate the plankton in both marine and freshwater habitats. Aquatic crustaceans are extremely valuable because in addition to including many of the larger arthropods, they are tremendously ecologically important in marine and freshwater food chains. Several species of crustaceans live above the high tide line on beaches but a comparatively small number are terrestrial. They have not been very successful as terrestrial animals because they have retained a characteristically aquatic physiology and are therefore restricted to damp environments. Several crustaceans live as parasites.

Crustaceans can generally be distinguished from the other groups of Arthropods by the possession of two pairs of antennae, and by the presence of **biramous** limbs. Crustaceans are almost entirely aquatic, with only a few hundreds of about 40,000 known species living on land; most species have free-swimming planktonic larvae. The plasticity in the structure of crustaceans has enabled them to swim, burrow, crawl, bore into wood, live cemented to rock, hunt, browse, suspension and deposit-feed, parasitise most animal groups, including their own. It is therefore no exaggeration to conclude that they occupy every type of marine niche.

3.2.1 The major crustacean characteristics

1. They are predominantly aquatic, with gills for respiratian.
2. They have five pairs of head appendages: (i) first antennae or antennules; (ii) second antennae; (iii) mandibles; (iv) first maxillae or maxillules; and (v) second maxillae.
3. The body is divided into different tagmata in the different groups, but usually has a recognizable head, thorax, and abdomen.
4. Exoskeleton often calcareous.
5. A posterior somite, the telson, contains the anus and bears no appendages.
6. They have a typical arthropod circulatory system with a heart having **ostia**, sometimes reduced in small forms.
7. The first, and in various groups, up to seven other trunk segments are fused with the head to form a **cephalothorax**.
8. The cephalothorax, and, in some groups, most or all of the body is enclosed in a carapace, which extends laterally and overhangs the sides of the body.
9. The excretory system contains antennal glands or maxillary glands or both.
10. A median eye and usually a pair of lateral eyes are present.
11. They are gonochoristic or rarely, hermaphrodite with internal fertilization through copulation by means of gonopods or penes; location of gonopore is variable but often thoracic.
12. Eggs usually carried by female or brooded inside specialised pouches; some hatch with full compliment of adult segments but some as **nauplius** larva.

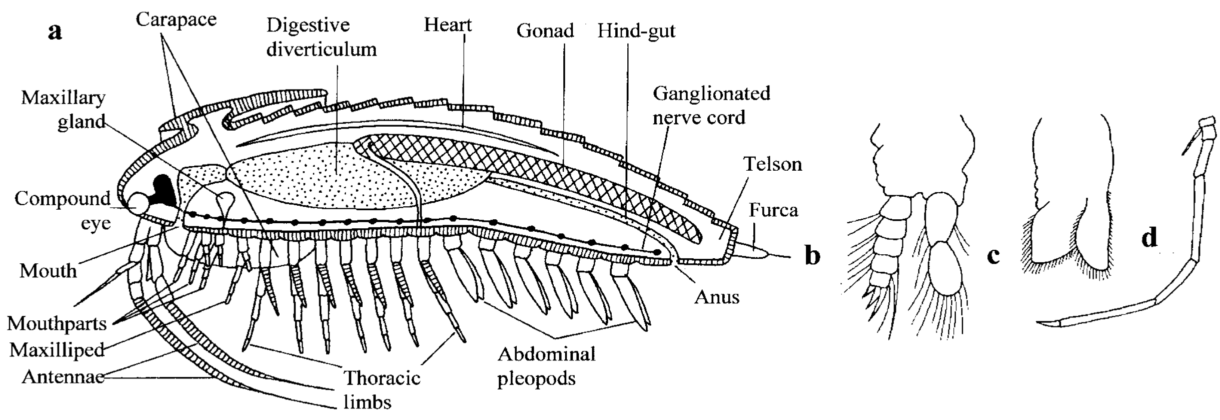


Fig. 10.1. Crustacean morphology. **a**, A diagrammatic longitudinal Section through the body of a generalized crustacean. **b, c & d,** Characteristic biramous limbs (greatly simplified). **b** has one tubular branch and the other leaf-like; **c** has two leaf-like branches – a typical swimming limb; **d** has two tubular branches – a typical walking leg. *Source:* Barnes *et al.* (1989).

3.3 Crustacean classes

The following nine classes of the subphylum Crustacea, which were listed in the table in the last unit, will be discussed very briefly:

3.3.1 Class Cephalocarida: Small, blind, less than 4mm long; detritus feeding, bottom dwelling. Body divided into head, thorax and abdomen without cepahalothorax or carapace. Usually hermaphrodite with paired ovaries and testes sharing common duct.

3.3.2 Class Branchiopoda: A diverse group of mainly freshwater crustaceans. Small to vestigial head appendages (except antennae); trunk segments are not fused to head; trunk segments with series of similar limbs that decrease towards posterior; last few segments lack limbs. Limbs bear gills and supported by hydrostatic pressure. Many are **parthenogenetic** and eggs are brooded.

3.3.3 Class Ostracoda: Very small, mostly marine, few terrestrial; less than 1mm long, rarely approaching 2mm. Short oval body enclosed in bivalved often calcareous shell formed by carapace; like some bivalve molluscs, the shell has adductor muscles for shutting the shell, but unlike them, the shell is shed at each moult. No external sign of segmentation.

3.3.4 Class Mystacocarida: Minute, less than 1 mm long, elongate, no pigment, marine; distinguished by head which is divided into small anterior and large posterior portion, and trunk of ten segments; first one bears a maxilliped even though it is not fused to the head. Head appendages are large and used in locomotion, trunk appendages are reduced, or are missing; the telson bears a large, pincer-like furca.

3.3.5 Class Copepoda: Dominant members of marine plankton and to some extent of that in fresh water as well. About 25% of all species are parasitic on animals ranging from sponges to whales. Most species are less than 2 mm long; however, one free-living species is about 2 cm and an ectoparasite about 0.3 m long. Basically, the body comprises a head, with well-developed mouthparts and antennae, thorax of six segments bearing swimming limbs, abdomen with five segments and no appendages. Parasitic species show various degrees of bodily degeneration, sometimes including loss of segmentation and appendages.

3.3.6 Class Branchiura: Small, less than 3 cm long. Periodic ectoparasites of marine and freshwater fish. They are dorso-ventrally flattened, with cephalothorax of head and first thoracic segment, a pereon of three segments, and a bi-lobed unsegmented abdomen; the cephalothorax and, in some, much of the pereon is covered by a large, flat carapace, and bears a pair of compound eyes. Head appendages are either minute or modified for attachment. All four pairs of thoracic appendages are wholly or partially incorporated into the cephalothorax and form swimming limbs; abdomen lacks appendages. The eggs are attached to substratum or vegetation.

3.3.7 Cirripedia: The most highly modified of the Crustacea, being either sessile or dwellers in other organisms in a parasitic manner. They are effectively headless, most lack an abdomen, and there is little or no evident segmentation. The order Rhizocephala resemble a bracket fungus, with a network of fine tubes spreading through all the tissues of the host and an external sac containing the gonads. The order Ascothoracica parasitize cnidarians and echinoderms and are the least specialized anatomically.

3.3.8 Class Malacostraca: By far the largest class, with about 23,000 species, and, it contains the greatest diversity of body form than all the other classes; just one of its 16 orders, the Decapoda, includes such varied organisms as crabs, crayfish, shrimps and hermit-crabs. Their main features are: a head, a thorax with eight segments, and an abdomen with six (or rarely seven) segments; all these regions are equipped with a full complement of segmental appendages, including the abdomen.

3.3.9 Class Remipedia: Represented by a single blind species only described from a marine cave, very little is known of its biology. Body is smallish, elongate and translucent, less than 3 cm long. Has a short cephalothorax of the head and first trunk segment; no carapace; long trunk of over 30 similar segments; swims upside-down. A pair of rod-like processes in front of antennules.

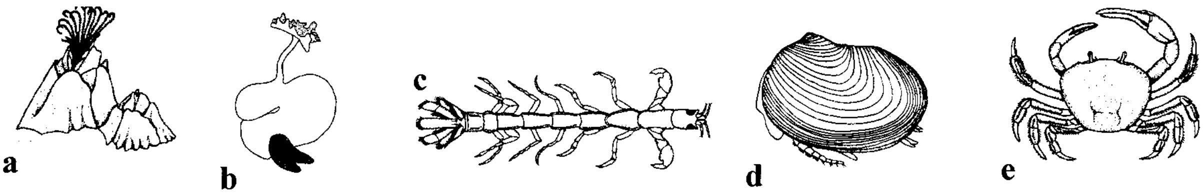


Fig. 10.2. Selected crustacean body forms: **a,** Acorn barnacles (Cirripedia); **b,** A parasitic copepod (Copepoda); **c,** An isopod (Malacostraca); **d,** A brachiopod (Brachiopoda); **e,** A crab (Malacostraca). *Source:* Barnes *et al.* (1989).

3.4 **Astacus*, a representative crustacean*** *(Class Malacostraca)*

Astacus illustrates most of the distinguishing features of the Crustacea that were listed/discussed earlier in this unit.

3.4.1 The exoskeleton

The external covering is formed by a segmented exoskeleton which is extremely thick and hard except at the **arthrodial/articular membranes**; this, as we saw earlier, is secreted by the single layer of epidermal cells. The surface layer, the epicuticle, is thin and composed of tanned lipoprotein, giving impermeability to the entire structure. The endo-cuticle is thick and composed of three layers: an outer pigmented layer of sclerotized protein, a middle layer of deposited calcium carbonate and an inner uncalcified layer (refer also to the structure of arthropod integument treated in unit 9).

4.0 Conclusion

The subphylum Chelicerata is much smaller than the Crustacea in terms of number and diversity; the chelicerates are more restricted in their distribution than the crustaceans. The majority of crustaceans are marine with only a few freshwater and even fewer, terrestrial.

5.0 Summary

Chelicerates include familiar animals such as ticks, spiders scorpions and mites. The first pair of appendages of chelicerates are called chelicerae, the second pedipalps and the rest four pairs are for walking. Chelicerae are feeding appendages. The body is divided into the prosoma and opisthosoma. Chelicerates lack antennae, mandibles and maxillae. About 40,000 crstacean species are known, distributed between nine classes, out of which over 75% are marine. The group is made up of crayfish, shrimps, crabs, barnacles, e.t.c. Crustaceans are distinguished from other arthropods in having two pairs of antennae and biramous appendages; they use gills for respiration.

6.0 Tutor Marked Assignment

1). What are the chelicerates named after and what is its use?
2). How many chelicerate classes are there?
3). Name the chelicerate classes.
4). In a tabular format, distinguish between the classes of the Chelicerata.
5). Name two crustacean classes and make one statement on each.

7.0 References/Further Reading

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Module 2: Coelomate Invertebrates II

Study Unit 3: Phylum Arthropoda *continued*

Contents

Study Unit 3

THE PHYLUM ARTHROPODA (ARTHROPODS) *continued*

1.0 Introduction

This study unit is a continuation of the last unit. In that unit we briefly discussed the attributes of the three classes of the subphylum Chelicerae and examined the diagnostic features of the subphylum Crustacea. We also selected *Astacus*, a malacostracan crustacean, as a representative of the subphylum, for detailed study. In this unit, we shall look at the organisation of *Astacus* and some of its systems. .

The exoskeleton and the general morphology of *Astacus* conform very closely with the general features of the arthropods and the subphylum, respectively. In studying the features of this crustacean, we should bear in mind the features of the various groups that we have examined so far: it is triploblastic, coelomate, a protostome, an invertebrate, an arthropod and a crustacean. We should not loose sight of the fact that it is bilaterally symmetrical, highly cephalized and metamerically segmented and look out for features that are indicative of these attributes, all of which we learnt in the preceding study units.

In this study unit, we shall discuss the body organisation and other features of *Astacus*, as reference material for the arthropods and crustaceans in particular.

In discussing the body organisation, we should note that: each tagma of an arthropod, including those fused together, typically bears a pair of jointed appendages. In the head region, one or two pairs are modified into long sensory structures called antennae and/or antennules. Tooth-like jaw appendages called mandibles are also usually present. Maxillae are limbs in the head region that are modified to pass food to the mouth. Most of the other appendages are used for walking or swimming; gills may be attached to the legs in aquatic forms.

2.0 Objectives

By the time you complete this study unit you should be able to:

- Appreciate the morphology of *Astacus* a representative crustacean.
- List the different types of appendages and their functions in *Astacus*.
- Describe the body organisation of male and female *Astacus*.
- Discuss aspects of locomotion, respiration, circulation and excretion in *Astacus*.
- Know the structure of the digestive system and process in *Astacus.*

3.0 Body organisation of *Astacus* (Fig. 11.1)

Astacus can be divided into three regions or tagmata, the head (consisting of six segments), thorax (eight segments) and abdomen (six segments with a posterior telson); the head and thorax are almost indistinguishably fused as a **cephalothorax** covered dorsally by the carapace. A cephalic groove roughly indicates the demarcation between head and thorax dorsally, and ventrally, some signs of external segments are visible. An accurate assessment of the number and position of the segments can be made from the appendages which are one pair per segment. The appendages are modified in response to specific feeding or sensory functions. The head extends anteriorly as a pointed **rostrum**, with a stalked eye lying on either side. In *Astacus*, the least specialized appendages, the **pleopods** or **swimmerets** occur on the first five abdominal segments. The exoskeleton of the abdomen also shows the least modification, with each segment consisting of a ring formed from a dorsal **tergite** (tergum) and a ventral **sternite** (sternum) (see the features of the arthropods in unit 9). The tergites overlap dorsally whereas the sternites are joined by a wide region of flexible membrane. The pleopods are **biramous** and attached ventrally to the abdomen by a **protopodite**; the latter is composed of a **coxopodite** (coxa) and a **basopodite/basipodite** (basis). The two branches attach to the basipodite, an outer **exopodite** and an inner **endopodite**, and both are fringed with bristles or setae. The appendages of the head and thorax, as well as the other abdominal appendages are modifications of this basic structure, either by loss of parts (the appendage becoming secondarily uniramous) or by addition of parts.

In <u>female</u> *Astacus* the first five <u>abdominal</u> appendages are all similar to the basic structure described except that the first pair is reduced in size. In the <u>male</u>, first pair is reduced to an unjointed rod and the second being stiffened, as modifications for sperm transfer. The endopodite of the sixth pair of abdominal appendages is modified in both sexes to form a broad fan-like structure, the **uropod** whose protopodite has a single segment, and both the endopodite and exopodite are greatly expanded. In combination with the telson, they form an effective rudder and swimming appendage; they act in combination with the strong contraction of the abdominal muscles, for rapid backward swimming when necessary.

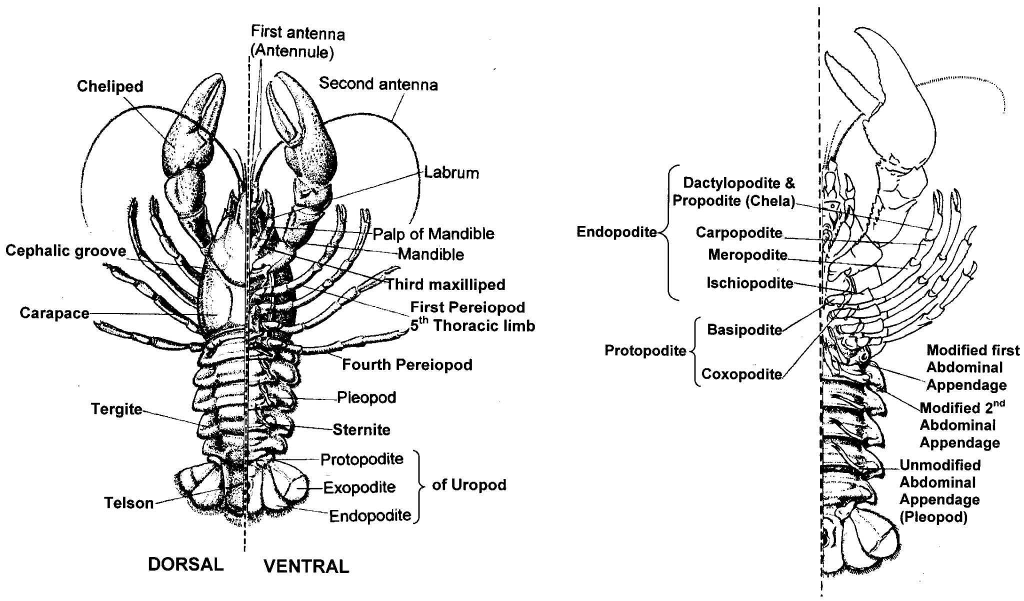


Fig. 11.1. Body organisation of *Astacus*: Dorsal and ventral views of **female** (**Left**); Ventral view of **male** (**Right**). *Source:* Kershaw (1988).

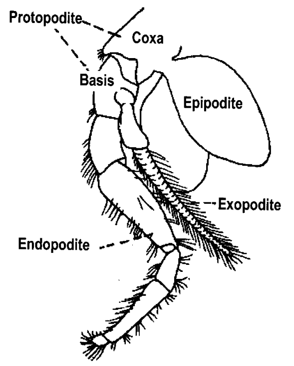


Fig. 11.2. Basic structure of a crustacean appendage. *Source:* Barnes (1980).

<u>Note</u>: The propodite is the sixth joint of the typical leg of a crustacean; Protopodite is basal part of a biramous appendage and consists of the coxopodite and basopodite/basipodite/basis

The <u>head</u> bears <u>five pairs</u> of appendages. The most anterior are the **first antennae**, or **antennules** which are relatively short and have two filaments borne on a peduncle of three segments. The second pair lies posterior to the stalked compound eye; (remember that the possession of two antennae is a diagnostic feature of the crustaceans, as we saw in unit 10). The endopodite of the antennae is represented by a long segmented filament and serves as a sense organ; the exopodite is a basal plate which controls the angle at which the animal dives. The head is also has three pairs of feeding appendages surrounding the ventrally located mouth. A pair of short heavy **mandibles** (segment 4) with opposing surfaces for grinding covers the mouth, which has a non-flexible labrum at the front. Behind these are two pairs of accessory feeding structures, the first and second maxillae. The first maxillae (segment 5) are small and flattened with two basal joints that are expanded and fringed with setae, and a reduced, unjointed endopodite. Both the coxopodite and basipodite of the second maxillae (or maxillules) (segment 6), are expanded as bilobed structures; the exopodite is also greatly enlarged as a **scaphognathite**, which acts as a paddle to create respiratory currents.

There are <u>five pairs</u> of <u>thoracic</u> appendages. The most anterior are the first **maxillipeds**, with their coxopodites and basipodites extended inwards; the endopodites form a broad plate and a tiny, two-jointed structure, and the exopodites are expanded into a long, many-jointed filament. The second and third maxillipeds each bear a pair of gills on the coxopodite. The exopodite is slender, with many segments, while the endopodite is large with five joints (named from the base: **ischiopodite**, **meropodite**, **carpopodite**, **propodite**, and **dactylopodite**), each bearing setae. The same joints and gills are found in the posterior thoracic appendages, but these all lack exopodites. The first pair, the chelipeds, are the longest and most conspicuous limbs of *Astacus*, with the protopodite and **dactylopodite** modified as a pair of huge pincers or **chelae**. The four posterior thoracic appendages, the walking legs or **pereiopods (pereopods)**, are similar except that the anterior two pairs bear small pincers while the others have a pair of simple spines.

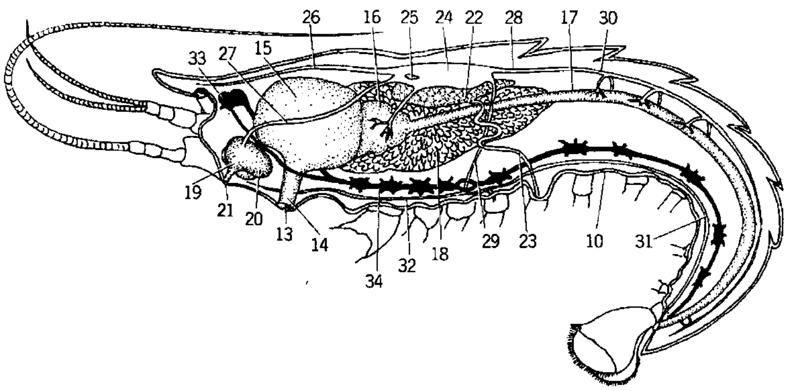
3.1 Locomotion

Astacus generally walks on its walking legs (pereiopods), holding its chelipeds out in front to counter-balance the weight of the abdomen. Movement is helped by a rhythmic anterior-posterior beat of the pleopods (swimmerets), which are chiefly used for swimming. Unlike many crustaceans, *Astacus* cannot swim using the pleopods alone as these are disproportionately small for its size. If startled, it retreats by darting backwards abruptly, as a result of the sudden flexure of the abdomen with the uropods and telson acting together as a paddle. *Astacus* is incapable of darting forward. The rapid nervous co-ordination for this activity is provided by a giant fibre system, similar to we saw in the annelids.

3.2 The digestive system and nutrition

Astacus has a straight gut with an anterior end highly modified for grinding. There are no cilia, and food is moved entirely by peristalsis. The mouth leads into a **stomodaeum**, lined with chitin, and consisting of a short oesophagus and a voluminous **proventriculus**, which has two chambers. The first (**cardiac**) chamber has a series of chitinous teeth and articulating plates, moved by muscles, which together form a gastric mill where food is crushed and ground. The second (**pyloric**) chamber (15, 16 in diagram) forms a sieve with rows of chitinous setae; here, the food is ground into extremely fine particles before it is passed down the alimentary tract into the **midgut**. This grinding protects the midgut from damage by abrasion, and also allows *Astacus* to have a very broad and unselective diet.

Astacus comes out of hiding to feed at night. Food consists of almost anything organic, animal or plant, alive or dead; it will eat snails or insect larvae, and frequently feeds on shells or calcareous algae for their calcareous content. During the coldest times of the year *Astacus* retreats into a burrow and does not feed. The process of transferring food into the mouth involves six pairs of appendages (the mandibles, maxillae, maxillules, and first, second and third maxillipeds) and therefore is complicated. The third maxillipeds are the largest and are used for picking up and tearing food; apart from its use in food acquisition, it protects the other appendages when the animal is not feeding. During tearing, the torn pieces are grasped by the mandibles and pulled by the second maxillipeds and with the aid of the first maxillipeds, passed forward to the mandibles. The food is then further broken up by forward and backward movements of the mandibles, and then pushed into the mouth by the maxillae.
Ingested food is broken down mechanically; chemical digestion occurs in the **stomodaeum**. A large bilobed digestive gland, the **hepatopancreas** (18 on the diagram), which consists of numerous finely-branched tubules, lies in the haemocoele and opens into the midgut. A watery dark-brown mixture of protease, carbohydrase and lipase is produced and sucked forwards into the cardiac chamber by dilator muscles, through paired ventral canals protected by a setal sieve. Digestion therefore starts in the gastric mill, and when it is sufficiently advanced, partly digested food and fine particles are passed back along the ventral canals into the pyloric chamber. This is tubular, the most anterior region acting for storage, and the next as a press in which partially digested and liquid matter is squeezed out. Digested food is absorbed in the hepatopancreas which is also used for storage of food reserves. Indigestible matter is passed along to the midgut and eventually leaves the anus via the cuticle-lined hindgut (proctodaeum). The anus opens in the ventral mid-line of the telson.



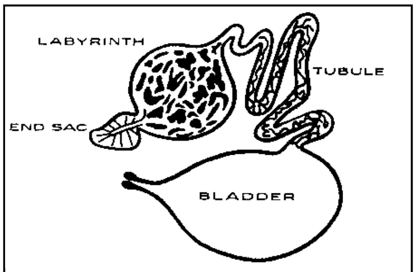


Fig. 11.4. The green gland (Antennal gland) of Crayfish.
Source: Barnes (1980)

Fig. 11.3. Scheme of internal organization of crayfish (male)

KEY
Digestive system: 13, mouth; 14, esophagus; 15, cardiac stomach; 16, pyloric stomach; 17, intestine; 18, digestive gland. **Excretory system:** 19, green gland (antennal gland); 20, bladder; 21, excretory pore**. Reproductive system:** 22, testis; 23, sperm duct**. Circulatory system:** 24, heart; 25, ostium; 26, ophthalmic artery anterior aorta; 27, antennary artery; 28, dorsal abdominal artery; 29, sternal artery; 30, segmental artery; 31, ventral abdominal artery; 32, ventral thoracic artery. **Nervous system:** 33, brain; 34, ventral nerve cord. *Source:* Meglitsch (1967).

3.3 Gaseous exchange

Astacus has developed a series of outgrowths (epipodites) which function as gills and have only a thin cuticle separating the blood from the respiratory current, this compensates for the restriction of permeable surfaces imposed by an exoskeleton. It has eighteen pairs of gills crowded into a branchial chamber formed by lateral extensions of the carapace, known as **branchiostegites**. The ventral surface of the branchial chamber is provided by the bases of the limbs, from the second maxilliped to the posterior end of the thorax.

Two types of epipodites occur, which are arranged in three layers. The **pleurobranchs** and **arthrobranchs** arise from the side of the thorax and from the articulatory membrane between the leg and the body, respectively. They both have a feather-like structure with a main stem (which carries the afferent and efferent blood vessels) bearing closely set branchial filaments on each side. The **podobranchs** arise from the coxopodites of the appendages and are double structures; the anterior branch is feather-like and the posterior plate-like. There is considerable variation in the arrangement of gills among crustaceans.

Water current is essential for successfully gill function. The current flows forward and is created by rhythmic sculling of the scaphognathites (second maxillae) which has a pumping effect. Water enters between the limb bases and at the posterior margin of the carapace; the gills are arranged to curve towards the current. The direction of flow is reversed periodically, to wash debris off the gill surfaces.

Gaseous exchange takes place in the thin-walled gill filaments which together provide a large surface area. The blood contains **haemocyanin** in solution, which functions in a similar way to haemoglobin. The pigment is blue-green in colour due to its copper content. Oxygen is taken up and transported, both in combination with the haemocyanin and in physical solution. Roughly 60 to 70% of the oxygen available in solution in the water current can be taken up by the crayfish.

3.4 The circulatory system *(see Fig. 11.2)*

Astacus has an open circulatory system, therefore its main organs lie and are bathed in blood within the blood-filled haemocoel, like in all arthropods, as we saw earlier. On the dorsal side of the thorax the haemocoel forms a large pericardial space (sinus) surrounding the heart. The heart is a muscular structure, polygonal in cross section and held in position by six strands of elastic fibres. After each contraction of the heart muscles these fibres cause it to expand again. Blood enters the pericardial sinus laterally from the gills, and passes into the heart by three pairs of **ostia** (antero-dorsal, lateral, and ventral). The ostia open passively when the heart expands to admit blood. Blood leaves the heart through seven arteries which convey it to the various blood-filled spaces in which the organs that lie in them are bathed. At the entrance to each artery there is a pair of valves that blood from flowing back into the heart when it expands.

A median anterior artery (**the ophthalmic artery**) extends forwards to supply blood to the brain, antennules, and eyes; near its anterior end it has a contractile dilation which functions as an accessory heart. In many small crustaceans this may be the only artery present. Two lateral antennary arteries supply the antennules, antennae, the green glands, and the anterior region of the alimentary canal. A pair of **hepatic arteries** leaves the heart latero-ventrally, to supply the digestive gland and gonads. A median **dorsal abdominal artery** from the posterior end of the heart extends along the abdomen and supplies the abdominal muscles and intestine. The **sternal artery** also leaves the heart posteriorly and descends to the ventral region of the body where it divides into two branches; one of these, the **ventral thoracic artery**, extends anteriorly, and the other, the **ventral abdominal artery**, extends posteriorly. A series of blood vessels, branch off these vessels, to supply haemocoeles within the appendages. Blood passes from the various spaces into large ventral sinuses and on to the gills, from where it goes back to the heart.

3.5 Excretory system (see Figs 11.2 & 11.3)

The principal osmoregulatory organs in *Astacus* are the paired **green/antennary glands** that lie in the haemocoele anterior to the mouth. They contain a rudiment of the coelom and are sometimes called coelomoducts. The glands are made up of a ventral glandular region over which lies a large, thin-walled bladder that opens through a duct in the base of the coxopodite of the antenna. The glandular region has an inner sac that is partitioned; this leads to a green labyrinth of cells from which a coiled **nephridial canal** leads to the bladder. Blood is supplied to capillaries within the inner sac by the antennary artery, and it is believed that ultrafiltration occurs between the inner sac and the blood; salts are reabsorbed in the nephridial canal. The green glands are therefore able to regulate the salt/water balance in *Astacus*. The urine formed, which collects in the bladder, is **hypotonic** to the blood. Nitrogenous waste, which for the most part is ammonia, is expelled through the gills. Small amounts of amino-nitrogen (10%) and urea are also excreted.

4.0 Conclusion

Astacus is a crustacean with its body divided into two main regions. It is a coelomate invertebrate whose coelom is reduced, the main body cavity being a haemocoel. It is a good representative of the subphylum Crustacea.

5.0 Summary

The body of crustaceans is divided into a cephalothorax and an abdomen. Distinguishing features of the crustaceans are: a cephalothorax covered by a carapace, biramous appendages, two pairs of antennae,three types of paired chewing appendages and various pairs of legs. The gut is more or less a straight tube and food is moved along by peristalsis. Gaseous exchange is through gills and the circulatory system is open. The excretory organ is the green/antennary gland and the excretory product is mostly ammonia.

6.0 Tutor Marked Assignment

1). What is the cephalothorax?
2). In one word, describe the uniqueness of crustacean appendages.
3). How many segments do the thoracic appendages of crustaceans have? Name them.

4). Write a brief description of the osmoregulatory structures of *Astacus*.
5). What is the haemocoel?

7.0 References/Further Reading

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Module 2: Coelomate Invertebrates II

Study Unit 4: Phylum Arthropoda *continued*

Contents

Study unit 4

THE PHYLUM ARTHROPODA (ARTHROPODS) *continued*

1.0 Introduction

From what we learnt in units 9 to 12, we can describe arthropods as bilaterally symmetrical, metamerically segmented, with chitinous exoskeleton, paired jointed appendages (of which at least one pair is modified as "jaws"), a haemocoel and a dorsal heart. In the last unit, we discussed the external features and some aspects of the anatomy and biology of *Astacus*, a typical crustacean. In discussing the internal organisation and the excretory and circulatory systems, we observed the reduction of the coelom with the development of a haemocoel (refer to study unit 1).

In this study unit, we shall conclude discussion on the organisation and biology of *Astacus*, which we selected as the representative crustacean. We shall examine the sensory structures and nervous system of *Astacus*, and the economic importance of crustaceans. In addition, we shall introduce the subphylum uniramia, which is the largest of the four subphyla of arthropods.

2.0 Objectives

After the completion of this study unit, you should be able to

- Describe the nervous system and sensory structures in *Astacus*.
- Appreciate the life history and importance of crustaceans
- Appreciate the basic differences between uniramians and other arthropods.
- List the characteristic and special features of the uniramians.
- Recognize the morphology of uniramians through the generalized forms.

3.0 Nervous system and sense organs of Astacus (refer to Fig. 11.1 in unit 11)

The arthropod central nervous system closely resembles that of annelids although the former shows a higher degree of cephalization. *Astacus* has a double ventral nerve cord whose strands are separate over most of their length but are linked by segmental ganglia that show some degree of fusion. The brain forms a ring round the anterior end of the alimentary canal; it is formed by cerebral ganglia (which lie anterior to the mouth) connected to the sub-oesophageal ganglion (formed by the fusion of ganglia: segments 4 to 8) by a pair of circum-oesophageal commissures. The remaining thoracic and abdominal ganglia are separate structures in segments 9 to 19. The cerebral ganglia receive nerve fibres from the antennae, antennules and eyes; the sub-oesophageal ganglion controls all mouthparts except the third maxillipeds.

Astacus has a well-developed system of giant fibres that are comparable with those of the annelids i.e. two median fibres extend from the brain to the telson, and two laterals arise segmentally and are not connected to the brain. The giant fibres provide nerves to the longitudinal abdominal muscles causing sudden rapid flexure, and also bring about sudden movements of the abdominal and thoracic appendages and antennae. The whole system provides a very effective escape reaction, as we mentioned earlier, in connection with locomotion.

Astacus has very well-developed sense organs. It has compound eyes of the type found among the arthropods, which are capable of detecting not only different light intensities but of forming images. These are large and prominent, and made up of about 2,500 units called **ommatidia** (sin. ommatidium), each pointing in a slightly different direction. An ommatidium is essentially a self-contained light-sensitive unit capable both of refracting light and of initiating nerve impulses which are transferred to the cerebral ganglion via the optic nerve. Its outermost region is a biconvex lens composed of transparent cuticle that is shed and replaced when the animal moults. The structure of the ommatidia is such that it permits vision under different light intensities.

Balancing organs or **statocysts** are very important in aquatic crustaceans such as *Astacus.* These are in the form of sacs, which open to the outside through a tiny pore at the base of the antennules. Each sac is lined with sensory hairs and contains the **statolith**, a bunch of sand grains that move around hitting against the sensory hairs, causing impulses to be sent to the brain. Whenever the animal moults, the statolith is lost along with the cuticular lining and has to be replaced with suitable grains picked up by the antennae and introduced through the openings of the statocyst.

Setae which respond to touch and **chemoreceptors** occur on the mouthparts as well as on the antennules and antennae. The antennae are particularly important as they can be held forwards or bent posteriorly to gain information ahead and behind as the animal moves.

3.1 Reproductive system and reproduction

The sexes are separate in *Astacus,* like in most crustaceans. The reproductive organs are a pair of testes or ovaries joined to form a Y-shaped structure; they give off two anterior canals that extend to the sides of the pericardial space, and a single posterior canal. In the female the two short ducts open near the bases of the second pair of walking legs. The walls of the oviducts are responsible for secreting a protective chitinous shell over the eggs. In the male the sperm ducts are long and highly convoluted, and open at the bases of the fourth walking legs. The glandular lining secretes a sticky substance which surrounds the sperm while in the sperm ducts. The sperm have no tails and are star-shaped with many spines.

Mating takes place shortly after the female has undergone her pre-adult moult. Male and female *Astacus* lie sternum to sternum, the male holding the female by his chelipeds and walking legs. The male uses his first two pairs of modified abdominal appendages to place and stick spermatophores onto the posterior sterna and pleopods of the female. When they come into contact with the water, the sticky secretion hardens and they may survive for a considerable length of time, up to a month.

External fertilization takes place after the partners have separated. The female lies on her back with her abdomen curved forwards to form a space, roofed by the abdominal terga with sides formed by long setae on the lateral margins of the terga. Eggs are discharged into the space, and moved about by a current produced by the beating pleopods. The sperm, released from the spermatophores, stick to the eggs by their spines and explode, firing their nuclei into the eggs. The fertilized eggs are cemented to special setae on the pleopods by a fluid produced by specialized glands, which forms a protective coat round each egg.

Development takes place within the yolky egg. The eggs are carried by the female until they hatch as miniature adults, lacking some abdominal appendages. They remain attached to the female's pleopods by specially modified, hooked chelipeds until they are fully grown.

The development of *Astacus* in which larval stages are omitted, is not common among crustaceans. Most crustacean eggs hatch into larvae which are totally unlike the adult and go through a succession of different larval forms to develop into the adult.

A free-swimming planktonic larva occurs in most marine and also some freshwater crustaceans, the earliest basic type being the **nauplius** (plural nauplii). It has only three pairs of appendages: two pairs of antennae and a pair of mandibles; it lacks trunk segmentation and has a single median or nauplius eye. The nauplius moults and metamorphoses into the other larval stages depending on the crustacean order. When the first eight pairs of trunk appendages are free of the carapace, the larva in higher malacostracans is called a **zoea**. In crustaceans in which the earlier larval stages are not clearly defined from the earlier stages, the term postlarva is applied. The postlarva may be quite similar to the adult in general appearance. The basic developmental pattern of nauplius, zoea (or its equivalent), and postlarva is very frequently modified. The postlarval stages of different groups are quite distinctive, and are confined to certain groups, for example the **megalops** (megalopa) of crabs (Decapoda), and **cypris** larvae, which are found only in barnacles (Cirripedia). If the zoea is very unique, it may be designated differently e.g. the **mysis** of lobsters. The intermediate stages also have different names; for example, the later nauplius **instars** (forms between moults) are called **metanauplii** (singular: metanauplius), and the pre-zoeal instar is called a **protozoea**. Crustacean development and metamorphosis rarely includes all the recognised larval types; a sequence of just two or three types is more common.

The larval stages which have been identified among crustaceans and discussed above are shown in Fig. 12.1 below.

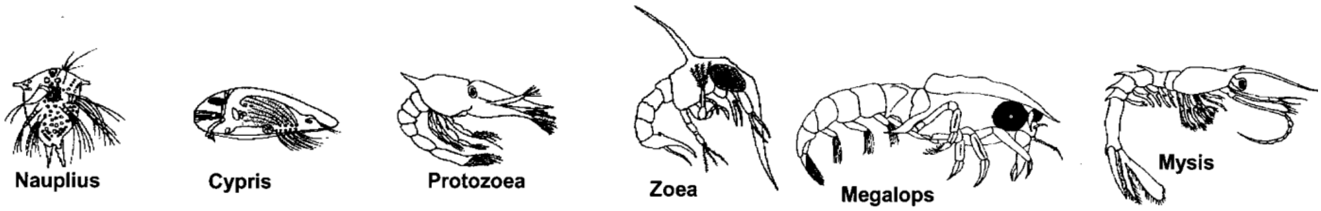

Fig. 12.1. Larval stages of crustaceans. *Source*: Meglitsch (1967).

3.2 Importance of crustaceans

3.2.1 As food

The crustaceans that are most obviously beneficial and important to humans are the larger edible species, mostly decapods.

- Marine shrimps, prawns, lobsters and crabs are valuable sources of food, and thus of considerable economic importance to fishing industries throughout the world.
- The most highly prized decapods are the true lobsters which are regarded as delicacies both in North America and in Europe.
- Freshwater crustaceans, including crayfish and some river prawns and river crabs, have local market value in many parts of the world.
- The large acorn barnacle (*Balanus psittacus*), measuring up to 27 cm in length, is regarded as a delicacy in South America, and a stalked barnacle (*Mitella pollicipes*) is eaten in parts of France and Spain.

- In Japan, barnacles are allowed to settle and grow on bamboo stakes, later to be scraped off and crushed for use as fertilizer.
- Planktonic (i.e., drifting) copepods, such as *Calanus* and *Euphausia*, may occur in such great numbers that they discolour large areas of the open sea and indicate to fishermen where shoals of herring and mackerel are likely to be found.
- The water flea (*Daphnia*) and the brine shrimp (*Artemia*) are used as fish food in aquariums and fish ponds, and the larvae of the latter are widely used as food for the larvae of larger crustaceans reared in captivity.
- Shrimps are used as components of livestock feeds as a source of calcium.

3.2.2 As pests/parasites

- In parts of Asia much damage may be done to rice paddies by burrowing crabs and mud-eating shrimps of various species. By undermining paddy embankments, they allow water to drain away, thus exposing the roots of the plants to the sun, and in coastal areas salt-water may be allowed to seep into the paddies.
- Tadpole shrimps (*Triops*) are often numerous in rice fields, where they stir up the fine silt in search of food, killing many of the plants.
- In some areas, land crabs and crayfish sometimes invade and damage tomato and cotton crops.
- The stalked goose barnacles (*Lepas*) often attach themselves to boats below the waterline, and encrust them heavily, necessitating periodic dry-docking of vessels in order to scrape and clean the hull.
- Parasites may destroy hatchery fish.
- There a number of important crustacean parasites of aquatic vertebrates, particularly fish, and invertebrates. Copepods parasitic on fish gills (e.g. *Ergasilus* and *Lamproglena*) may cause loss of gill tissue thus impairing respiration. The copepod *Lepeophtheirus salmonis* is a parasite of major economic importance in fisheries. Another example, *Sacculina* (Cirrepedia), parasitizes crabs; infestations by them cause castration resulting in infertility in the crab.
- The isopod *Livoneca* infects and sucks blood from the skin and gills of fish.
- Some crustaceans serve as intermediate hosts to parasites of humans and wildlife.

3.3.3 Uses other than for food

- Crustaceans are important primary and secondary consumers in many aquatic systems, and are especially crucial in limnetic waters (the lighted surface water in a lake with no rooted aquatic plants).
- Some species support direct fisheries and aquiculture for human food or fish bait, important fish and wildlife foods.
- Some may help control unwanted aquatic vegetation,
- Many are good environmental indicators for metals, acid rain, global warming, etc.

3.3 Subphylum Uniramia (Latin: **unus***, one;* **ramo***, branch)*

The subphylum Uniramia is characterized by individuals with uniramous (single-branched) appendages (as the name implies), one pair of antennae and two pairs of mouthparts (single pair each of mandibles and maxillae). The Uniramia are primarily terrestrial, although many species have secondarily invaded freshwater, a few have reinvaded the marine environment and one group has the ability to fly. Uniramia includes millipedes, centipedes and insects. Onychophorans were formerly included in the Uniramia but they are now placed in a separate phylum; we shall very briefly discuss their relationship with the arthropods. Uniramians are by far the most common and diverse major group of arthropods, making up over 75% of all known animal species. Like the crustaceans, they are very important both economically and ecologically.

3.3.1 Diagnostic and special features of the subphylum Uniramia

1. Bilaterally symmetrical; < 1 mm-35 cm long arthropods varying in body shape from extremely elongate to almost spherical.
2. Body more than two cell layers thick, with tissues and organs.
3. A through, straight gut without digestive diverticula (.
4. Body divided into two regions, a 'head' and three or four appendage-bearing segments, and a 'trunk' bearing pairs of walking legs; in one class, the trunk comprises a series of up to 350 relatively uniform segments, most of which bear walking legs; in the other class, the trunk is differentiated into a 'thorax' with three pairs of legs, and an 'abdomen' of up to eleven segments with highly modified appendages, if any.
5. Appendages are uniramous, those of the head include one pair each of 'antennae', 'mandibles', and maxillae, and in some groups a second pair of maxillae, those of the trunk all form functional or modified walking legs; without chelicerae or chelate limbs.
6. Two or three pairs of mouthparts (the mandibles and maxillae); members of each pair work with or against the other; the bases of the maxillae, or second maxillae in those groups have two pairs, which fuse to form a plate flooring the pre-oral cavity (the labium or 'lower lip').
7. Head with lateral ocelli, frequently organized into compound eyes; sometimes also with median ocelli.
8. Trunk, but not head, externally segmented.
9. Most members of one class with one to two pairs of wings on the thorax.
10. With a fat body in the haemocoel, often closely associated with the gut.
11. Excretory system: none to two pairs of maxillary glands in the head, and 1-75 pairs of unbranched ectodermal Malpighian tubules arising from the hind-gut near its junction with the mid-gut and discharging mainly ammonia and/or uric acid.
12. Exoskeleton calcareous or, more commonly, non-calcareous.
13. Gaseous-exchange organs paired, branched tracheal tubes through which air diffuses.
14. Blood without any circulatory function in respect of the respiratory gases, and without respiratory pigments (except in a few larval stages).
15. Gonochoristic, with internal fertilization through spermatophores or copulation.
16. Several groups with a distinct larval stage; others hatching with less than the full complement of segments (and legs), additional segments being added at each moult.

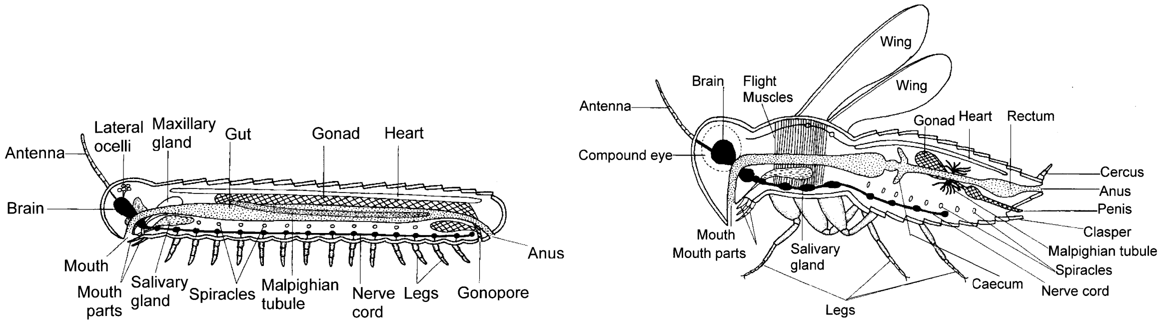

Fig. 12.2. Diagrammatic longitudinal sections through two generalized Uniramia: **Left**, Myriapod; **Right**, Hexapod (insect). *Source:* Barnes *et al.* (1989).

3.3.2 Phylum Onychophora (Velvet worms)

- These are terrestrial caterpillar-like animals; about 12cm long.
- They possess a combination of arthropod and annelid characters and have been described as a "missing link" between both groups; they have also been described as "living fossils".
- They occur in damp forests beneath logs of woods, leaves and beneath the bark of rotten logs.
- They are largely nocturnal and avoid light.
- They are found in Australia, Tasmania, New Zealand, New Guinea, South Africa and Chile.
- The best known is *Peripatus*. By 2004, there were about 155 species distributed among 47 genera.

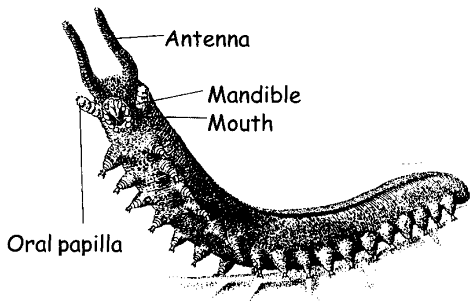

Fig. 12.3. *Peripatus*, an onychophoran. *Source:* Kershaw (1988).

4.0 Conclusion

The nervous system of arthropods resembles that of annelids. Reproduction in *Astacus* excludes larval stages, unlike other crustaceans. Crustaceans are both beneficial and detrimental.

5.0 Summary

The brain of *Astacus* is in form of a ring of ganglia around the anterior part of the alimentary canal. Most crustaceans are monoecuous and fertilization is external. Astacus does not have any larval stages but most crustaceans do. Larval stages identified among crustaceans include: Nauplius; Protozoea; Zoea; Megalopa (Megalops) and Mysis. Crustaceans form important links in both aquatic and terrestrial food webs. There are several important pests and parasites among crustaceans. The subphylum Uniramia is made up of arthropods with unbranched appendages. There are two general body forms of uniramians: myriapodod type and hexapod (insect) type.

6.0 Tutor Marked Assignment

List the sense organs of crustaceans and mention their functions.

List the larval stages of the different crustacean groups.
List five ways each, in which crustaceans are beneficial and detrimental.
What is an instar?

7.0 References/Further Reading

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Module 2: Coelomate Invertebrates II

Study Unit 5: Phylum Arthropoda *continued*

Content

Study Unit 5

THE PHYLUM ARTHROPODA (ARTHROPODS) *continued*

1.0 Introduction

The phylum Arthropoda is very large, as we have observed in the last four study units; it is so large, diverse and important that a whole course is usually devoted to its study. In unit 12, we completed some aspects of the organisation and biology of the crustaceans and discussed some ways in which they directly and indirectly affected humans; in the same unit, we introduced the subphylum Uniramia, the last of the four arthropod subphyla and very briefly mentioned the phylum Onychophora, which until recently, was a class in the phylum Arthropoda. We discussed the special features of the uniramians with the aid of generalised diagrams of the two main types. In this study unit, we shall list the characteristics of the classes Chilopoda, Diplopoda, Symphyla and Pauropoda, all of which are described as myriapods (many feet), and discuss the Insecta in greater detail.

2.0 Objectives

- ❑ Characterise the myriapodous uniramians
- ❑ Appreciate the basic differences between the major arthropod groups.
- ❑ List the characteristics of myriapodous arthropods
- ❑ List the characteristic and special features of the class Insecta.
- ❑ Characterise insects by their orders.
- ❑ Appreciate the body form of insects.

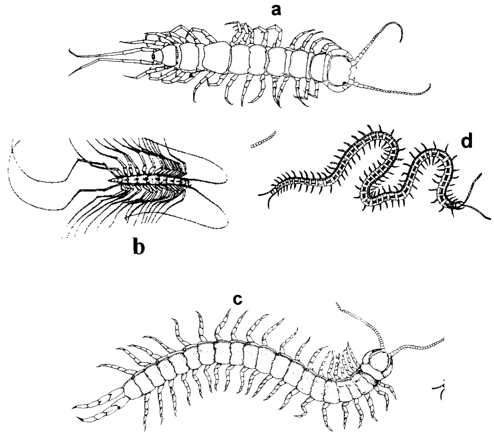
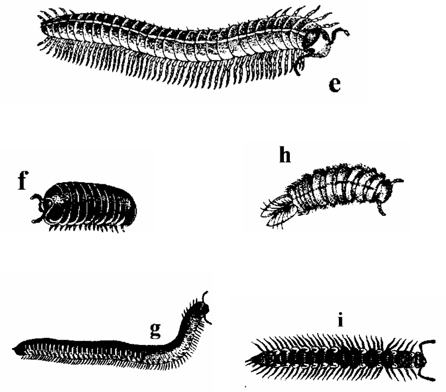
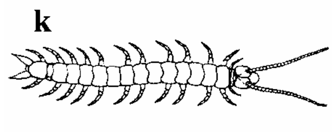
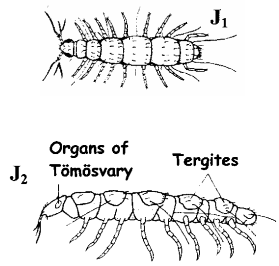
3.0 Myriapodous arthropods[‡] (Myriapoda means many footed).

- They are terrestrial with one pair of antennae and many pairs of walking legs.
- Their bodies consist of a head and a long trunk.
- They lack a waxy epicuticle and are prone to desiccation; they therefore live in humid areas.
- True compound eyes are absent, simple eyes are often present.
- Respiration is by means of trachea.
- Excretion is by means of Malpighian tubules.
- Sexes are separate.
- Young resemble adults but have fewer segments.

Table 13.1. Classification of the myriapodous uniramians with examples of the different classes

Class	**Figures of Examples**

[‡] The term myriapod is used here as a descriptive term for many-footed arthropods. Myriapoda is regarded as a subphylum by many workers and as a class by some. Myriapodous arthropods include the Chilopoda (centipedes), Diplopoda (millipedes) and two other small groups, Symphyla and Pauropoda.

Class	Figures of Examples
Diplopoda ♦ Commonly known as millipedes. ♦ Each apparent segment bears 2 pairs of legs (Diplopoda). ♦ The first four segments represent the thorax, which bear one pair of legs each. ♦ No appendages on the first trunk segment. ♦ The genital pore is in the third thoracic segment. ♦ They are sluggish and sensitive, often coiling up when disturbed; they also do this for protection. ♦ They are cosmopolitan in the tropics hiding under leaves, stones, logs etc. ♦ They generally keep away from light. ♦ They are herbivorous.	 **a,** *Lithobius*; **b,** *Scutigera*; **c,** *Scolopendra*; **d,** *Geophilus*.
Chilopoda ♦ They are commonly known as the centipedes. ♦ The body is dorso-ventrally flattened. ♦ The trunk segments are numerous (15-177). ♦ Each trunk segment except the last two bears a single pair of legs. ♦ The first trunk segment bears poison claws or maxillipeds, which cover the other mouthparts. ♦ The cuticle is elastic and not strengthened. ♦ The genital pore is located at the posterior end of the body. ♦ They are fast moving and do not coil but also live under leaves, bark of trees, beneath stones and around the house. ♦ They are carnivores.	 **e,** *Chordeuma* **f,** *Glomeris* (pill millipede); **g,** *Julus*; **h,** *Polyxenus*; **i,** *Polydesmus*.
Symphyla ♦ They are small, less than 8 mm long. ♦ They are morphologically similar to the centipedes. ♦ The leg-bearing segments are not more than 12. ♦ They have a single pair of legs per leg-bearing segment. ♦ A single pair of tracheae that open through spiracles on the head. ♦ They are blind. ♦ They are herbivorous.	 *Scutigerella*
Pauropoda ♦ They are minute, less than 2 mm long. ♦ They live in the same habitat as symphylans and millipedes. ♦ They feed on fungal hyphae. ♦ They are morphologically similar to the millipedes. ♦ The head bears two maxillae. ♦ The first two and last two trunk segments have no legs. ♦ They have no heart. ♦ They have no tracheae. ♦ They have branched antennae. ♦ They are blind and colourless. ♦ They all belong to one order.	 *Pauropus*: Dorsal view (J_1) & Lateral view (J_2).

3.1 *The class Insecta*

3.1.1 Insect diversity

Insecta is the largest class of animals, in terms of number of species: Nearly one million have so far been described, and it is believed that several times that number remain unknown to science. Although only a few species are marine (and none have been found in the deep ocean), insects are dominant in almost every terrestrial and freshwater ecosystem, and they occupy nearly every ecological niche available to animals (herbivores, carnivores, internal and external parasites, detritivores, etc.). Insects are also called hexapoda, which means "six feet," a very familiar insect characteristic.

3.1.2 Characterisation and distinguishing features

Insects are characterized by three pairs of legs, two pairs of wings, a single pair of antennae, and a pair of compound eyes. Their bodies are protected by an exoskeleton of sclerotized cuticle and divided into three regions: head, thorax and abdomen.

The main external body features that are unique to the four major Classes of living arthropods: crustaceans, myriapods, arachnids and insects, are shown in Table 13.1. All the features that are listed for insects are not shared by the other arthropod groups and are therefore unique.

Table 13.1. The major arthropod classes and their distinguishing external morphological features

Group	Main body regions	Pairs of legs	Pairs of antennae	Wings
Crustacea	**Two:** cephalothorax and abdomen (some with head & trunk)	**Five** or **more**	Two	Absent
Myriapoda	**Two:** head and trunk	**Many**; one or two per trunk segment	One	Absent
Arachnida	**Two:** cephalothorax & abdomen (prosoma & opisthosoma)	**Four**	None (palps may resemble antennae or legs)	Absent
Insecta	**Three:** head, thorax & abdomen	**Three**	**One**	Usually **present** (but many are **wingless**)

3.2 *Classification of insects*

Insects are generally recognised and studied by their orders, so the first thing to do when trying to identify an unknown insect is to determine its correct order. This can be done for many common insects with the aid of a hand-lens and a simple key. Insects are placed in 29-34 orders, 31 of which are listed in Table 13.2 below; the subclasses of insects and their features are also indicated. The number of insect orders varies with different classification schemes; this is the reason why a range of numbers has been given here for the number of orders. Over 85% of insect species belong to four of the orders, which are quite familiar: the beetles (Coleoptera); the flies (Diptera); the moths and butterflies (Lepidoptera); and the wasps, bees and ants (Hymenoptera). Despite their number and diversity, insects are less diverse than crustaceans.

Table 13.2. Insect orders with their subclasses and features
(*Source*: modified from http://www.kendall-bioresearch.co.uk)

ORDER	COMMON NAME	SUBCLASSES & FEATURES
1. Thysanura	Bristletails; silverfish	**APTERYGOTA** These are wingless insects and their body structure suggests that they have never had wings during their evolutionary history. Young stages resemble the adults - no metamorphosis (**ametabolous**). Their mouthparts are partially enclosed within the head capsule/withdrawn into head.
2. Diplura	Two-pronged Bristletails	
3. Protura	-	
4. Collembola	Springtails	
5. Ephemeroptera	Mayflies	**PTERYGOTA** **Division EXOPTERYGOTA** These are winged insects, although some have lost their wings during the course of evolution. When present, the wings develop externally and there is no marked change (metamorphosis) during the life cycle. The young stages, called nymphs, resemble the adults except in size and in lacking fully-developed wings – **paurometabolous/ simple/gradual/incomplete metamorphosis**. Mouthparts protrude from the head.
6. Odonata	Dragonflies	
7. Plecoptera	Stoneflies	
8. Grylloblattaria	-	
9. Orthoptera	Crickets, Grasshoppers & Locusts	
10. Phasmida	Stick and Leaf Insects	
11. Dermaptera	Earwigs	
12. Embioptera	Web-spinners	
13. Dictyoptera	Cockroaches and Mantids	
14. Isoptera	Termites	
15. Zoraptera	-	
16. Psocoptera	Psocids or Booklice	
17. Mallophaga	Biting Lice	
18. Anoplura	Sucking Lice	
19. Hemiptera	True Bugs	
20. Thysanoptera	Thrips	
21. Homoptera		
22. Heteroptera		
23. Neuroptera	Alder Flies, Snake Flies and Lacewings	**PTERYGOTA** **Division ENDOPTERYGOTA** These are winged insects, although some have lost their wings during the course of evolution. When present, the wings develop internally (i.e. inside the body of the immature insect) and there is a marked change (metamorphosis) during the life cycle. The young stages are very different from the adults and are called larvae. The change from larva to adult takes place during a non-feeding stage called the pupa (or chrysalis) – **complete metamorphosis/holometabolous.** Mouthparts protrude from the head.
24. Coleoptera	Beetles	
25. Stresipstera	Stylopids	
26. Mecoptera	Scorpion Flies	
27. Siphonaptera	Fleas	
28. Diptera	True Flies	
29. Lepidoptera	Butterflies and Moths	
30. Tricoptera	Caddis Flies	
31. Hymenoptera	Bees, Wasps and Ants	

3.3 Characteristics

In addition to characteristics listed in Table 13.1, insects have the following characteristics:

- A pair of compound eyes.
- The thorax is divided into **prothorax, mesothorax** and **metathorax**, each has a pair of walking legs ventrally.
- The mesothorax bears a pair of wings dorsally, which are non-membranous and not used in flight; these wings are called **elytra** (sin. elytron).
- The metathorax has a pair of membranous wings dorsally that are used for flight.
- The abdomen consists of eleven segments with no walking legs.
- Respiration is by means of trachea.
- Excretion is by means of Malpighian tubules.
- Insects undergo metamorphosis, which involves abrupt changes of form.

(Note that there are wingless insects as indicated in Tables 13.1 & 13.2).

We shall now examine a fairly typical and common insect, the grasshopper, as a representative of the class, just as we did with the other groups of coelomate invertebrates.

3.4 Body organization of the grasshopper

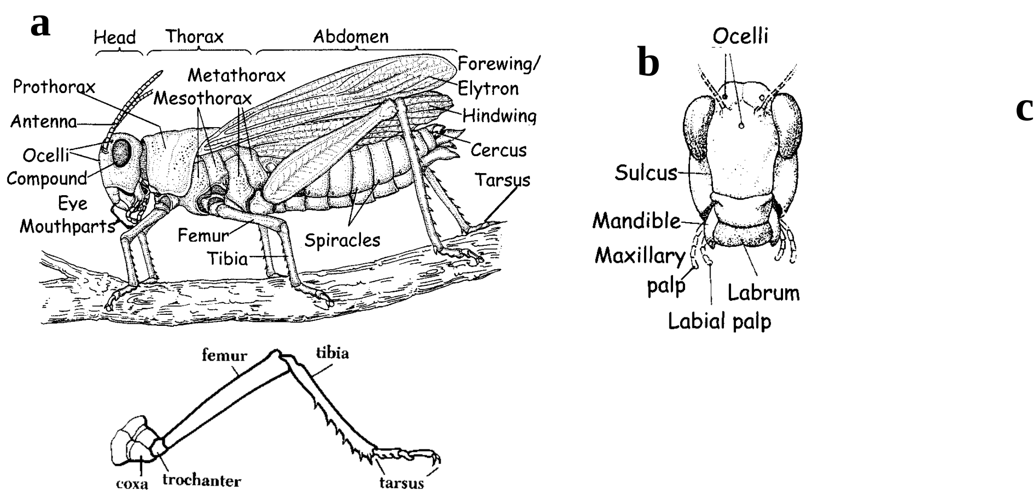


Fig. 13.1. The grasshopper: **a**, Lateral view; **b**, the head showing mouthparts; **c**, middle leg showing parts of a typical insect leg. *Sources*: Mitchell *et al.* (undated); Kershaw (1988); Buchsbaum (1989).

The head of a grasshopper has two **compound eyes** and three simple ones. The compound eyes are similar in structure to those of the crayfish (examined in unit 11), although not borne on a movable stalk as in the latter, they have a broad field of vision because they occupy a large area and curve around the sides of the head. There are **four pairs** of head appendages: first, a pair of long, jointed sensory **antennae**; secondly, hard toothed jaws (**mandibles**); thirdly, a pair of accessory mouthparts (**maxillae**), each with a jointed sensory palp; and fourthly, fused into a single plate, the **labium**, with a sensory palp on each side, forms the lower lip of the mouth. The upper lip (labrum) is a simple hardened outgrowth in front of the mouth and is not formed from paired appendages, as the labium. The head is covered by a hard conical capsule, and its segmentation is indistinct in the adult, but the four pairs of appendages show that it has about 4-6. The segments are obvious during embryonic development and conform also to the situation in crustaceans

The thorax bears three pairs of legs, a character of all insects. The thoracic segmentation is partly concealed dorsally by a chitinous shield and by the wings, but the three thoracic segments are clearly visible ventrally and laterally. The legs are jointed and each one ends in two curved claws flanking a fleshy pad and aid in clinging to smooth surfaces. The first two pairs of legs are typical walking legs, like those of most insects. The third pair is specialized for jumping; the **femur** is enlarged and contains muscles for jumping. Two pairs of wings are located on the second and third segments of the thorax; the **forewings** (elytra) are narrow and hardened, and they serve as a cover for the hindwings. Both pairs are used in flying. The **hindwings** are broad and delicate, spread wide in flight, but folded like a fan to fit under the first pair when the grasshopper is at rest. The wings are made of cuticle and are stiffened by hardened structures called veins.

The abdomen has appendages only at the posterior end; they are associated with mating and egg-laying. The abdomen contains most of the soft internal organs. It is rounded in cross section and made up of 11 segments, the eleventh being fused to the tenth and only discernible in embryos.

4.0 Conclusion

Uniramians are the myriapods and insects. Insecta is the largest class of arthropods but it is not as diversified as the crustaceans. The class is immediately distinguishable from the other major arthropod classes.

5.0 Summary

The myriapodous uniramians are accommodated in four classes: Diplopoda, Chilopoda, Symphyla and Pauropoda. Insects have three pairs of legs, two pairs of wings, a single pair of antennae, and a pair of compound eyes. Their body is divided into three: head, thorax and abdomen. Insect development can be ametabolous, paurometabolous, or holometabolous.

6.0 Tutor marked Assignment

1) Classify and characterize the insects on the basis of wing development alone.

2) Make a good sized labelled drawing to show the structure of a typical insect leg.
3) Briefly describe the structure of the head of a grasshopper.
4) Name the appendages of the insect's thorax.

7.0 References/Further Reading

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Module 2: Coelomate Invertebrates II

Study Unit 6: Phylum Arthropoda *continued*

Contents

Study Unit 6

THE PHYLUM ARTHROPODA (ARTHROPODS) *continued*

1.0 Introduction

This is the last study unit of our discussion on the arthropods. At the end of the last unit, we started discussing the grasshopper as a typical insect; in this unit, we shall conclude the discussion and also examine factors that contribute to the success of insects and their economic importance.

2.0 Objectives

After completing this study unit, you should be able to:

- Understand how insects carry out some of their vital functions.
- Know the structure of the digestive, excretory, reproductive and nervous systems.
- Appreciate the factors that contribute to the success of insects.
- Appreciate the economic importance of insects.

3.0 The exoskeleton

This is the same as described for the arthropods. In the grasshopper, the sclerites of the head fuse to form the head capsule.

3.1 THE SYSTEMS

3.1.1 The digestive system (Fig. 14.1)

The digestive tract consists of **foregut**, **midgut**, and **hindgut**. The foregut and hindgut are lined with cuticle, which is shed and renewed with the exoskeleton at each molt. The foregut of a grasshopper contains special regions that cut and grind the quantities of vegetation that make up the diet. The midgut, lies mainly in the abdomen, has no cuticular lining; it serves as the main organ of digestion and absorption. The junction of the midgut with the hindgut is marked by the attachment of long excretory tubules. Thus the hindgut receives the waste materials of digestion and excretion.

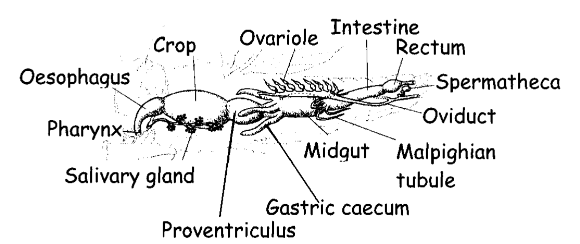

Fig. 14.1. The digestive, excretory and repro-ductive systems of the locust/grasshopper. *Source:* Kershaw (1988).

The foregut starts at the mouth, receives a secretion from the **salivary glands**, and continues as a narrow esophagus, which leads to the **crop**, a large thin-walled sac in the thorax. On the inner walls of the crop are transverse ridges armed with rows of spines that probably serve to cut the food into shreds. The crop is mainly a storage sac that enables a grasshopper to eat a large quantity at one time and afterward digest it leisurely. From the crop the food passes into a muscular **gizzard/proventriculus** lined with chitinous teeth. At the posterior end of the gizzard is a valve that prevents the food from passing into the midgut before it is thoroughly ground and also prevents food in the midgut from being regurgitated. Digestion begins in the crop, (or the food entering that organ is already mixed with salivary secretion, and it also receives some digestive juices that pass anteriorly from the midgut. Six pairs of pouches, **gastric caeca** which secrete digestive juices open into the anterior end of the midgut, they also aid in absorption. The hindgut, which consists of the pylorus, intestine and rectum, transports waste matter to the anus and it is an important site for reabsortion of salts, amino acids and especially water; the latter is a significant factor in survival of terrestrial insects.

3.1.2 The excretory system (Fig. 14.1)

The excretory system consists of a number of Malpighian tubules that lie in the blood sinuses and extract nitrogenous wastes from the blood. Fluid from the tubules is poured into the hindgut, from which much of the water and some salts are reabsorbed. The material remaining is mostly crystals of **uric acid** that are expelled from the anus as dry waste. This system resembles that of spiders and serves the same important function of water conservation.

3.1.3 Gaseous exchange system (Fig. 14.2)

The gaseous exchange system is highly developed in insects and composed of air tubes called **tracheal tubes**. The tubes lead from paired openings, called **spiracles**, which lie at the sides of the thorax and abdomen. The ten pairs of these openings are guarded by fine hair-like bristles that keep out dirt and by valves that open or close to regulate the flow of air. Closure of the valves aids in decreasing evaporation of water. The air tubes are prevented from collapsing by spiral thickenings in the cuticular lining of their walls.

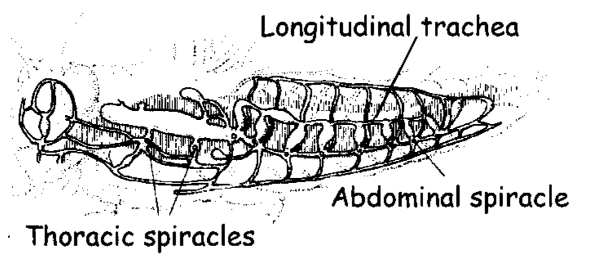

Fig. 14.2. The tracheal system of the locust/grasshopper. *Source:* Kershaw (1988).

Smaller branches radiate to all parts of the body, from a system of longitudinal and transverse main trunks, and eventually become so small that groups of the finest ones (**tracheoles**) are made by a single cell. Here and there the larger tubes widen into air sacs. The air moves chiefly by diffusion, but muscular breathing movements, which alternately compress the air sacs and then allow them to expand, assist in gaseous exchange. The greater the muscular activity increases the pumping action on the air sacs, and facilitates the circulation of air. In a grasshopper the first four pairs of spiracles open only at inspiration and the remaining six pairs open only at expiration; this facilitates air flow. In the deepest branches, oxygen moves by diffusion alone, first along the tubes, and then into the surrounding blood spaces and tissues. Carbon dioxide leaves by the reverse route. Small amounts of oxygen and carbon dioxide also may be exchanged through thin parts of the body surface.

3.1.4 The circulatory system (Fig. 14.3)

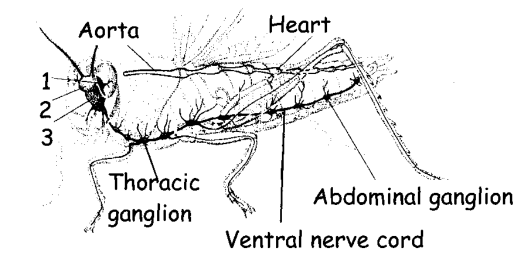

Fig. 14.3. Circulatory and nervous systems of the locust/grasshopper. **Key:** 1, Protocerebrum; 2, Deuterocerebrum; 3, Tritocerebrum.

The circulatory system does not carry respiratory gases so it is not very extensive. There is only one vessel, the long contractile dorsal vessel, composed of the tubular **heart,** which pumps the blood forward, and its anterior extension, the **aorta.** In each segment through which it passes, the heart is dilated into a chamber perforated on each side by a slit through which blood enters. Blood leaves the heart through a series of openings and through the aorta, which carries blood into the head and there ends abruptly. The blood flows out into sinuses among the tissues, bathes all the muscles and soft organs, and finally returns to the heart. Although the system is an open one, the flow is given some direction by a series of partitions, and the slow rate of blood flow is sufficient for the redistribution of food and collection of wastes. The blood is also a reservoir for food and water; it contains cells that destroy bacteria and other parasites; blood pressure plays a part in hatching, moulting, and expansion of the wings by filling the veins with blood.

3.1.5 The nervous system (Fig. 14.3)

The nervous system is comprised of a ventral, double, ganglionated cord. The brain, which is divided into the **protocerebrum**, **deuterocerebrum** and **tritocerebrum**, lies above the esophagus and between the eyes. It is joined to the first ventral ganglion by a pair of connectives that encircle the gut. The **brain** has no centers for coordinating muscular activity; if the brain is removed, the animal can still walk, jump and fly. In other invertebrates, the brain is a sensory relay that receives stimuli from the sense organs and responds by directing the movements of the body. The brain is also responsible for certain complex behavior patterns and for modifying them by learning. The **first ventral ganglion** controls the movements of the mouth parts and exerts a general excitatory influence. The **segmental ganglia** are connected and coordinated by nerves that run in the cords, but each is an almost completely independent center in control of the movements of its respective segment (or segments) and appendages. In some insects these movements have been shown to continue in segments that have been cut off from the rest of the body. An isolated thorax is capable of walking by itself, and an isolated abdominal segment performs breathing movements.

3.1.6 Sensory organs

The grasshopper, like all insects, has very well-developed sense organs. The **compound eyes** are large, with a basic structure similar to that described for crustaceans. In addition, three **ocelli**, two lateral and one median, occur, which detect degrees in light intensity and are very sensitive to low light. Other sense organs are scattered over the general body surface; they are particularly abundant on the appendages. They are said to be derived from setae, and consist of a receptor cell associated with cuticular modifications in chemoreceptors, which are concentrated on the mouthparts, antennae and legs; extensions of the receptor cells pass through fine pores in the cuticle, which is modified either as a peg or a hair. Various kinds of chemical stimuli are important in insect lives. They help them to recognize and locate their food, and recognize their own species for mating or social behaviour by means of **pheromones**. **Chemoreceptors** are extremely sensitive to the presence of pheromones and the animals can respond to the most minute traces (literally a few molecules), of such substances. There are various kinds of touch receptor such as a tactile hair, or a **campaniform sensillum**, a thin, domed area of cuticle above a single receptor cell. They are concentrated in groups in areas of the body subject to mechanical stress, such as the leg joints.

Grasshoppers are capable of producing sounds by **stridulation**, which involves scraping a ridge on the inner surface of the femur of the hind leg against a row of pegs on the **elytra** producing a loud noise in males; the wing pegs are reduced in the female, which is silent. Two **tympanal organs** occur, one on either side of the first abdominal segment for detecting sound. These consist of the tympanic membrane, backed by an air sac. The tympanic membrane vibrates and is associated with the specialized **chordotonal organs** organs which respond to changes of tension. These are formed by groups of **scolopida**, which are receptors stretched between two points beneath the cuticle. Apart from detecting sound, chordotonal organs may be found in the region of joints where they function as **proprioreceptors**.

3.1.7 Locomotion

Grasshoppers/locusts exhibit three methods of locomotion: walking, leaping and flying, to which the structure of the legs and wings are well adapted. This was briefly mentioned under “Body organization”. The grasshopper/locust uses short jumps to walk but it can leap to great heights as an escape mechanism. Insects are the only invertebrates that can fly; grasshoppers and locusts are very powerful fliers and migrate very long distances.

We shall not go into the details of the flight mechanism in this course.

3.1.8 Reproduction and development

The reproductive system of the grasshopper and other insects includes a pair of gonads and their associated ducts. A male grasshopper has a pair of testes, which discharge sperm into a sperm duct; glands secrete seminal fluid into the duct, which opens near the posterior end of the body. A female grasshopper has a pair of ovaries, with oviducts that join a common genital chamber. At copulation the male introduces sperms into the female's seminal receptacle, where they are stored until egg laying. When ripe, the eggs pass down the oviduct; yolk and shell are secreted around the still unfertilized eggs. A small pore, the micropyle, is left, through which a sperm may enter. As the eggs pass into the genital chamber, they are fertilized by sperm from the sperm receptacle. A conspicuous set of stout appendages, the ovipositors, near the posterior end of the abdomen, are used for digging a hole in the ground in which to lay the eggs. Most insects do not care for their eggs except selecting a favorable laying site, often a specific food plant or the body of an animal on which the young may feed when they hatch.

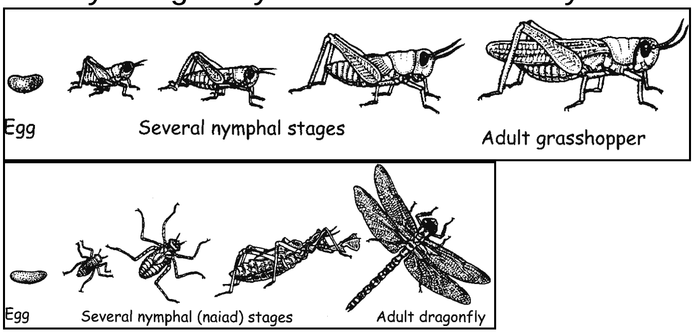

Fig. 14.4. Incomplete/paurometabolous/simple/gradual metamorphosis in the grasshopper and dragonfly. *Source:* Mitchell *et al.* (undated).

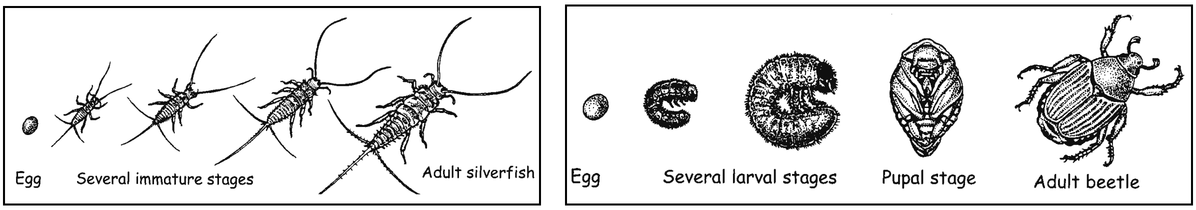

Fig. 14.5. Ametabolous development in the silverfish (Thysanura) and complete/holometabolous metamorphosis in a beetle (Coleoptera). *Source:* Mitchell *et al.* (undated).

The development of insects is strongly influenced by the large amount of yolk in the egg. The young grasshopper, known as a nymph, hatches out of the egg resembling the adult but with a disproportionately large head, and no wings and reproductive organs. It feeds on vegetation, grows rapidly, and moults five times in most grasshoppers, discarding the old exoskeleton. It is ruptured and shed, by a combination of muscular contractions and the uptake of quantities of water and air. The newly emerged insect is soft and white; and since it is delicate, it usually retires to a safe place until the soft cuticle hardens and darkens. With each successive molt, differentiation continues, until the final moult results in the adult form.

3.2 Social organization of insects

This fascinating account of the life of insects will not be complete if their social organization is not mentioned. Insects have very highly structured social organizations which are found within the orders Isoptera (termites), and the Hymenoptera (ants, bees and wasps). Different members of a colony are usually specialized for performing different tasks; each kind of individual belongs to a caste. Three different castes are often present:

1. Reproductive female – **Queen**.
2. Male/female **Workers**, involved in support, protection and maintenance of a colony.
3. Reproductive males – **Drones**.

The castes are regulated by pheromones released by queen. Social behavior includes concepts of selflessness and kin selection.

3.3 The success of insects

In terms of diversity and abundance, insects are the most successful group of animals and constitute about 75% of the known species of animals. Their success is attributed to:

1. Their small size, which enables them to escape from enemies and go undetected by predators. The small size also allows large numbers occupy a small space.
2. Ability to fly in some, enabling them to escape from danger.
3. Possession of a chitinous exoskeleton that is resistant to water loss thus preventing desiccation, enabling them to survive in the terrestrial habitat.
4. Possession of an efficient nervous system with numerous sensory organs like antennae, eyes, setae, etc. for detecting changes in their immediate environment.
5. They are well adapted to different habitats.
6. They are adapted to feeding on a wide range of food items (minimizes inter-specific competition for food) – even within a species, the larval stages and adults have mouthparts that are adapted to feeding on different food materials.
7. Their reproductive efficiency enables them to produce large numbers of eggs and offspring within a short time.
8. They produce resistant eggs.

3.4 Economic Importance of Insects

The activities of insects have impacted directly and indirectly, and positively and negatively on the existence of humans on earth. Most of the impressive statements that are made about arthropods especially the huge number of species, the remarkable economic importance, are really about insects. Their impact on humans is so much that they are often studied on their own under the subject of **entomology**.
The following are some ways in which they are **beneficial** to humans:

- ☞ Some are sources of food for humans e.g. honey from the honeybee; termites, grubs etc.
- ☞ They pollinate flowers and consequently aid in fruit formation, vegetation cover, etc.
- ☞ They produce important raw materials for industries e.g. silk from the silkworm.

- They constitute food for other animals in the biosphere e.g. lizards, toads and fish, all feed on insects.
- They help in the decomposition of dead organic matter by scavenging. E.g. dung beetles.
- They form important research tools (*Drosophilla*).
- Used in the biological control of some pests. E.g. Lady Birds used in aphid control.

Harmful effects

- Aphids and other homopterans feed on plant sap causing injury and destruction.
- Serve as vectors of bacterial and viral plant diseases.
- Some are vectors of important parasitic diseases of humans and animals e.g. tsetse flies (trypanosomiasis), the housefly (amoebic dysentery), mosquitoes (malaria) etc.
- They are parasites of humans and plants e.g. lice, fleas, bedbugs etc.
- Some insects attack stored food items and produce e.g. bean weevil, rice weevil etc.
- They destroy wooden structures in furniture, buildings, buildings, etc., e.g. termites, wood lice, carpenter bees etc.

NB: This list is not at all exhaustive; students and tutors are encouraged to add to the list.

- You should also note that there is a great deal of variation in all the features that we have examined above, depending on the lifestyle of the insects.

4.0 Conclusion

The organisation and vital functions of insects as a group are mostly reflected in the grasshopper. The grasshopper is indeed a typical insect.

5.0 Summary

Insects have a ventral nerve cord and a dorsally located heart which pumps blood through an open circulation system. The blood is rarely needed for oxygen circulation in the body. Tracheae regulate air exchange, and free amino acids play a major role in osmoregulation. Malpighian tubules rid the body of metabolic wastes. The sexes are separate and copulation is often the rule. Development in grasshoppers is paurometabolous. Insects are critical links in many food webs. Most flowers are insect pollinated. Many insects are parasites and vectors of diseases that cause human mortality. Insects are the most successful of the numerous arthropod groups, as a result of their size, high fecundity, ability to fly, feeding habits, etc.

6.0 Tutor Marked Assignment

1) Describe the structure of the digestive tract of the grasshopper.
2) Draw the head of the locust and label its mouthparts.
3) Enumerate four ways in which insects are beneficial to humans.
4) List five factors that are responsible for the success of insects
5) List two ways in which insects are harmful to humans.

7.0 References/Further Reading

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Module 2: Coelomate Invertebrates II

Study Unit 7: Phylum Echinodermata

Contents

Study unit 7

THE PHYLUM ECHINODERMATA (Greek: *echinos* = hedgehog; *derma* = skin i.e. spiny-skinned)

1.0 Introduction

The phylum Echinodermata is said to be a link between the invertebrates and the chordates because of certain similarities that the two phyla share.
The echinoderms and chordates are known as **deuterostomes** because in both groups, the blastopore of the embryo develops into the anus and the mouth forms at the opposite end. In the **protostomes** (annelids, molluscs, arthropods and their allies), on the other hand, the blastopore of the embryo gives rise to the mouth of the adult (this was discussed in study unit 1). It is believed that the echinoderms branched from the same deuterostome evolutionary stem as the vertebrates. Echinoderms are typically pentamerous, i.e. having five arms as seen in the starfish and on the sand dollar. They have a true coelom (see study unit 1). This is the last group of coelomate invertebrates that we are examining in this course.

2.0 Objectives

By the time this lecture unit is completed students should be able to:

- Appreciate the unique pentaradial symmetry of echinoderms.
- See how the general body plan of the echinoderms has been modified in each class.
- Note the relationship between the echinoderms and the chordates.
- Recognize the echinoderms by their distinguishing features.
- Describe the diversity of body form among the echinoderms.

3.0 Outstanding features of the echinoderms

- The structure of all living and most fossil forms is based on a five-sided (**pentamerous/pentaradial/pentaradiate**) symmetry (some of them have increased this number while some have regained bilateral symmetry). Since radial symmetry is a secondarily acquired character, the echinoderms are not related to radially symmetrical organisms.
- Their most outstanding feature is their planktonic bilaterally symmetrical larvae which develop into radially symmetrical adults; no other animal is known to do this.
- The spiny skin.
- They have a water vascular system.

In this lecture, we shall discuss the characteristics of the subphyla of the phylum Echinodermata.

3.1 Diversity of echinoderms

There are about 6,250 - 6,500 species of echinoderms distributed between three subphyl and five classes. They are exclusively marine.

3.1.1 Characteristics

1. They **pentaradially symmetrical coelomate** animals.
2. The early larva shows evidence of metameric segmentation; adults are unsegmented.
3. Adult is secondarily radially symmetrical.
4. There are **two** main types of body form among adults: **radiate** and **globular**.
5. They are not cephalized (without any differentiated head) but have oral - aboral axis.
6. Their body surface consists of five fields with podia (ambulacra) alternating with five that have no podia (interambulacra).
7. There are various forms of the gut and it might not have an anus.
8. Their nervous system is well developed but uncentralized. The system is made up of three nerve rings around the digestive tube with peripheral nerves radiating from them.
9. Body wall is made up of a ciliated epidermis underneath which is a dermis that contains calcareous ossicles, which give rise to spines.
10. The musculature of their body wall is poorly developed.
11. They have a simple circulatory or haemal system that runs through a system of coelomic compartments.
12. Their **coelom is large** and is in three distinct compartments.
13. A unique water vascular system is formed from one of the compartments of the coelom. This is said to be the most unique feature of the echinoderms.
14. The 'tube feet' (podia) are offshoots of the radial canals of the water vascular system and the suckers at their ends facilitate attachment to a substrate and are also used for locomotion.
15. No special organs of excretion.
16. Sexes are separate.
17. They have various forms of free-swimming and free-living larvae each associated with the different classes.

3.2 Classification

Table 15.1. Subphyla and Classes of the Echinodermata

Subphylum	Characteristics	Class(es)
Crinozoa	1) There are stalked and sessile larval and adult stages. 2) Tube feet, when present, are tentacular. 3) The anus is usually on the oral surface. 4) Mouth is directed upwards.	Crinoidea (Sea lilies & feather stars). E.g. *Antedon, Pentacrinus, Rhizocrinus*
Asterozoa	1) They are radially symmetrical, free-swimming (not stalked) and their bodies are star-shaped. 2) They have double sets of tube feet that typically have suckers at their ends. 3) The anus is usually on the aboral surface. 4) The mouth is directed downwards.	Asteroidea. E.g. *Xyloplax Asterias, Astropecten*
		Ophiuroidea. E.g. *Ophiothrix, Ophiura, Ophiocomina*
Echinozoa	1) They are globular in shape. 2) Arms are never formed. 3) Ambulacral grooves are closed. 4) The anus varies in position. 5) The mouth is directed either downward or forward.	Echinoidea. E.g. *Echinus, Spatangus*
		Holothuroidea. E.g. *Holothuria, Psychropotes, Labidoplax, Cucumaria*

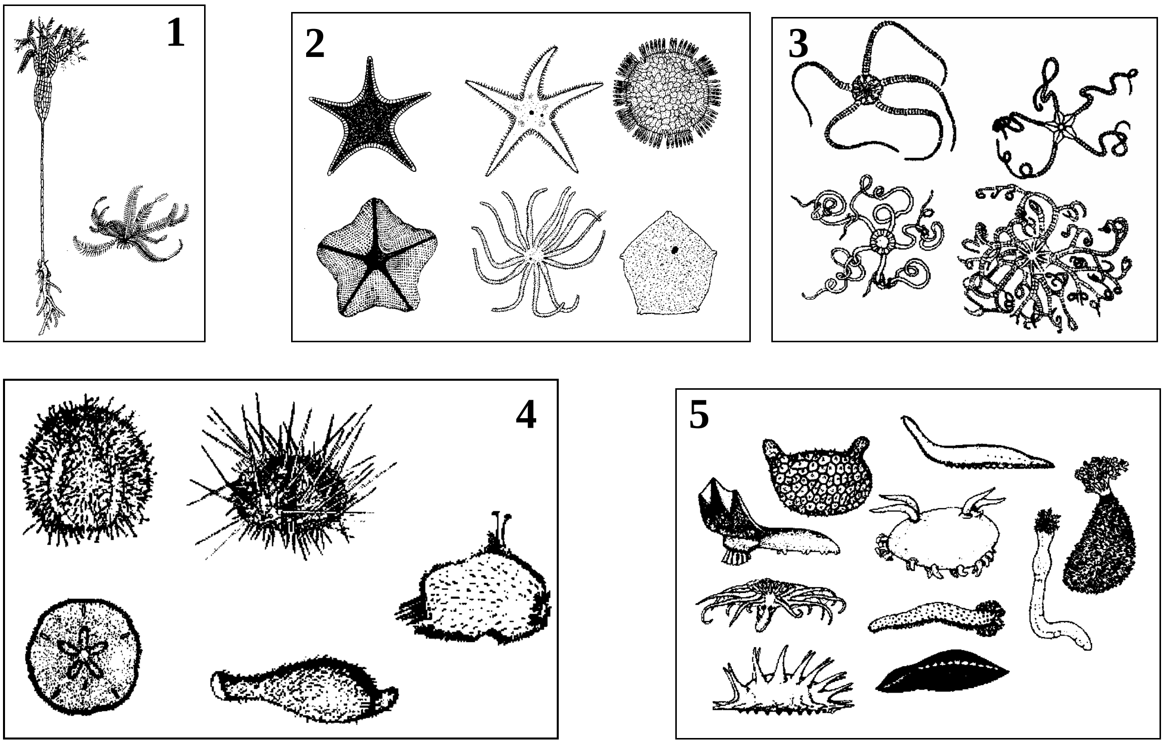

Fig. 15.1. Body forms of echinoderm classes: **1,** class **Crinoidea** (Sea lilies & feather stars); **2,** class **Asteroidea** (Starfishes/Sea stars; Sea daisies); **3,** class **Ophiuroidea** (Brittlestars and basket-stars); **4**, class **Echinoidea** (Sea urchins, sand-dollars, etc.); **5,** class **Holothuroidea** (Sea cucumbers). Source: Barnes *et al.* (1989); (2001).

3.3 Echinoderm organization

Despite the diversity of echinoderms observed above, most of them look very much alike and have similar modes of life. Almost all of them are scavengers and predators that feed on a variety of animals as they move slowly along the sea shore or bottom of the ocean. We shall discuss the organisation and biology of *Asterias* (sea star) as a representative echinoderm, because it is cosmopolitan.

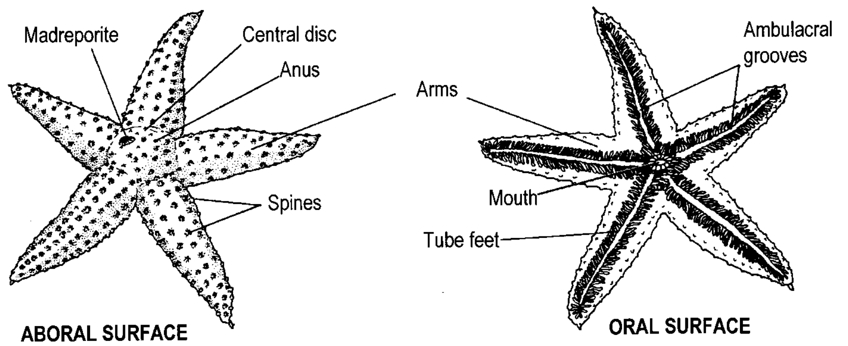

Fig. 15. 2. A starfish showing the aboral and oral surfaces.
Source: Modified from Mitchell *et al.* (undated)

3.3.1 Body form of *Asterias*

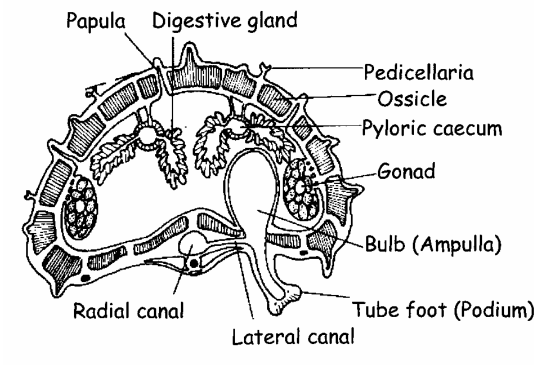

Fig. 15.3. T.S. of arm of *Asterias* showing associated structures. Note thedetails of the tube foot. *Source:* Kershaw (1988).

Asterias is star-shaped; it is strongly flattened along the oral-aboral axis and consists of a central disc from which project five blunt-tipped arms. The central disc bears the mouth in the centre of the lower (**oral**) surface, and an inconspicuous anus on the upper (**aboral**) face. Another opening, the madreporite, lies inter-radially near the centre of the aboral face and opens into the stone canal, an extension of the water vascular system. The aboral surface is brownish and covered with numerous irregularly arranged blunt spines; the oral surface is paler and has about 200 tube feet which project in two double rows in grooves (the ambulacral grooves) extending from the mouth along each arm. The grooves are protected by long stout ambulacral spines which are movable and can be held projecting downwards or across the groove. **Pedicellariae** (small pincer-like structures), occur on both the oral and aboral surfaces. Each pedicellaria is formed from three ossicles: a basal supporting structure, and a pair of ossicles which form the pincers or jaws themselves. One pair of muscles (the abductors) swing them open, and another pair (the adductors), close them. The jaws may cross each other, or touch at the tips. Pedicellariae may be fixed or stalked with a long reach and considerable flexibility. Stalked pedicellariae are particularly characteristic of the ambulacral grooves while those of the aboral suface are more usually fixed and are arranged in rings round the spines. Pedicellariae are used to remove detritus from the body surface, and also to kill and discard any small animals that touch them. By so doing, the starfish uses them to prevent sessile animals (e.g. barnacles) from settling on their body. Without pedicellariae a slow moving animal with a firm surface, such as a starfish, would be vulnerable to colonizers, as well as to small predators.

3.3.2 The body wall

The outermost layer of the body wall is thin and contains ciliated cells, mucous gland cells, and sensory cells covered by cuticle. The mucous cells secrete a protective coating while the epidermal cilia sweep off detritus. Immediately below the epidermis is a nerve plexus; and below this is a tissue in which the ossicles are embedded. These are formed of a mixture of calcium carbonate (90%) and magnesium carbonate (10%) and are three-dimensional matrices, with spaces filled by soft tissue, and are joined to each other by a network of collagen fibres. The oral wall ossicles are closely but flexibly fitted and those of the ambulacral grooves are particularly large for muscle insertion. In contrast, the aboral wall ossicles form an irregular lattice. The body wall is completed by inner longitudinal and outer circular smooth muscle fibres and by a layer of peritoneum.

3.3.3 The water vascular system

The **madreporite** opens into a small space, the ampulla, which leads via the vertical **stone canal** (so called from calcareous deposits in its walls), to a **ring canal**. The lumen of the stone canal is subdivided so that fluid can pass both orally and aborally. Five ciliated **radial canals** (one per arm) extend from the ring canal, and each ends in a sensory structure, the **optic** cushion, which is a modified **tube foot**. Lateral canals extend from each side of the radial canal, each opening into an aboral bulb (**ampulla**) and oral tube foot (**podium**). The opening is guarded by a valve. These canals are alternately long and short on each side so that the tube feet on either side are arranged in two rows. The radial canals and tube feet lie outside the main part of the body in the ambulacral groove, but the ampullae project into the body cavity. A total of nine **Tiedemann's bodies** arise inter-radially from the ring canal; the position of the tenth (expected from pentaradial symmetry) is occupied by the stone canal.

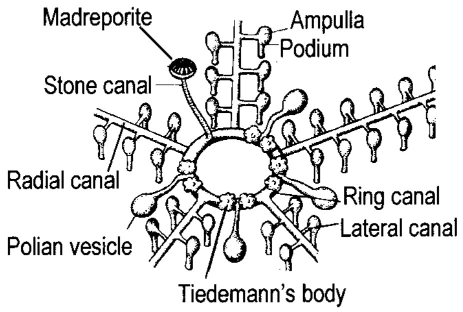

Fig. 15.4. The central part of the water vascular system showing associated structures. *Source*: Barnes (1980)

The podia have broad sucker-like tips and function hydraulically. Rings of smooth muscle in the wall of the ampulla contract, the lateral canal valve closes, and fluid is thus forced into the podium causing it to elongate. When the sucker of the podium touches a solid surface its centre is withdrawn producing a slight vacuum and therefore causing it to stick by suction. The epidermis of the sucker region has many sensory cells, as well as gland cells which produce a copious adhesive secretion. The podium wall is not impermeable and as it is extended some fluid is squeezed out. The madreporite is said to equalize internal and external pressure over the remainder of the water vascular system.

3.4 Locomotion

Asterias crawls slowly, with one arm leading; sometimes it may extend two arms in front or even lead with an inter-radial region. Any of the arms can be used to lead. Propulsion is provided by the tube feet which move in a series of steps (3-10 per minute). Each foot in turn is extended, fixed to the substratum, and used as a lever to push the body forwards. Muscles in the podial walls are used to retract the foot, as well as to orientate it during use, and provide the necessary suction for attachment. Many of these originate on the ambulacral ossicles. In addition the tube has a layer of connective tissue which prevents the foot from bulging rather than extending.

3.5 Feeding and digestion

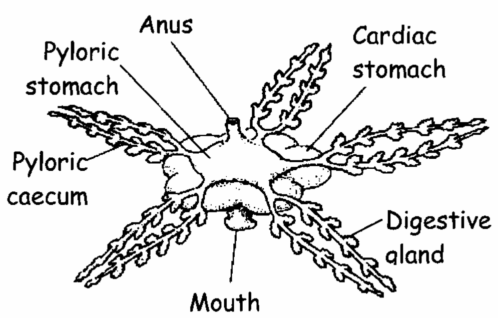

Fig. 15.5. Digestive system of *Asterias*. *Source*: Kershaw (1988)

The alimentary canal is aligned in the vertical axis, extending through the disc from the mouth on the lower side to the anus on the upper side. All the gut structures are surrounded by the coelom. The mouth, which is closed by a sphincter muscle, opens into a short narrow **oesophagus** and then a large, pouched, **cardiac stomach**. The walls of this stomach are connected to the ambulacral ossicles of the arms by ten pairs of triangular gastric ligaments. The cardiac stomach opens into the smaller **pyloric stomach**; this is flattened and appears star-shaped because of 10 blind-ending **pyloric caeca**, or digestive glands, which extend from it, one pair down each arm. A short common duct joins each pair to the pyloric stomach. The digestive glands are hollow ciliated structures made up of glandular cells that secrete enzymes and also function for food absorption and storage. From the pyloric stomach, a short intestine, from which

arise the short, blind-ending rectal sacs, extends to the anus.
Asterias is a predaceous carnivore and feeds mainly on bivalve molluscs, especially *Mytilus.* It holds the bivalve so that the non-hinged surface is held firmly pressed against its mouth, and attaches its arms to the valves by the tube feet. Retraction of the tube feet then forces the valves to open slightly. Once the shell is open *Asterias* everts part of its cardiac stomach into the prey. Proteolytic enzymes with lipase, amylase, and invertase are poured into the prey and a partly digested mixture is extracted from it. Fluid and particles are moved by ciliary action through the digestive tract and into the pyloric caeca where food is absorbed and stored.

3.6 Gaseous exchange, excretion, and circulation

Gaseous exchange takes place across the tube feet and small evaginations of the body wall called **papulae**. The tube feet and papulae are also the site for removal of the waste product, ammonia; echinoderms have no specialized excretory system. Since the body fluids are **isotonic** with sea water, osmoregulation is unnecessary. The fluid in the perivisceral coelom provides the main means of internal transport with the aid of its peritoneal cilia.
The haemal system in *Asterias* is poorly developed and consists of oral and aboral rings, a radial sinus paralleling the water vascular canal in each arm and a canal which parallels the stone canal and is surrounded by a mass of spongy tissue, the **axial gland**. The axial gland is said to destroy any micro-organisms which get into the body. The haemal system fluid contains **coelomocytes** which may play a role in food transport. A dorsal sac in the madreporite pulsates and functions as a heart.

3.7 Nervous system and sense organs

In addition to a sub-epidermal nerve net, which extends all over the body, *Asterias* shows some concentration of nerve fibres which form a nerve ring around the mouth. Five radial nerve cords arise from the nerve ring and extend along each arm; they are involved in the coordination of the podia. Additionally, the sub-epidermal plexus thickens to form marginal nerve cords that extend along the sides of the ambulacral grooves. The sub-epidermal system is predominantly sensory and a deeper system of fibres extends from the radial nerves to supply the body wall muscles, podial muscles and ampullary muscles.
Asterias has large numbers of epidermal tactile, chemical and light sensitive receptors scattered over the general body surface, but concentrated particularly along the margins of the ambulacral groove and on the podia. There is an optic cushion at the tip of each arm, formed from a collection of about 150 pigment cup ocelli. *Asterias* is distincly phototactic.

3.8 Reproduction and growth

The sexes are separate. *Asterias* has five pairs of gonads (ovaries or testes) which are suspended in the perivisceral coelom by strands of mesentery; they open through ciliated **gonoducts**, at a cluster of gonopores near the junction of the arms. The site and extent of the gonads varies seasonally; near spawning, they may almost fill the arms.
The sperm and eggs are shed into water, and fertilization is external. At a single spawning a female *Asterias* may release up to 2.5 million eggs in about two hours. The presence of eggs in the water stimulates the shedding of sex cells by other males and females. Shed sperm stick to the ova. After fertilization, the **dipleurula** larva develops, with a ventral mouth, and with an anus derived from the blastopore (the deuterostome condition). At first cilia are

widely distributed over the surface of the larva, but this soon reduces to a definite ciliary band, consisting of two longitudinal bands connected in front of the mouth and behind the anus. The characteristic larval stage of *Asterias* is a **bipinnaria** larva arrived at by the development of two groups of arms along which the ciliated bands extend. It is planktonic for several weeks and feeds on pelagic organisms such as diatoms. It eventually sinks and becomes temporarily attached to the substrate, and develops into a **brachiolaria** larva with three additional anterior arms and an adhesive sucker. It undergoes the final stage of metamorphosis, becoming sexually mature after about 12 months.

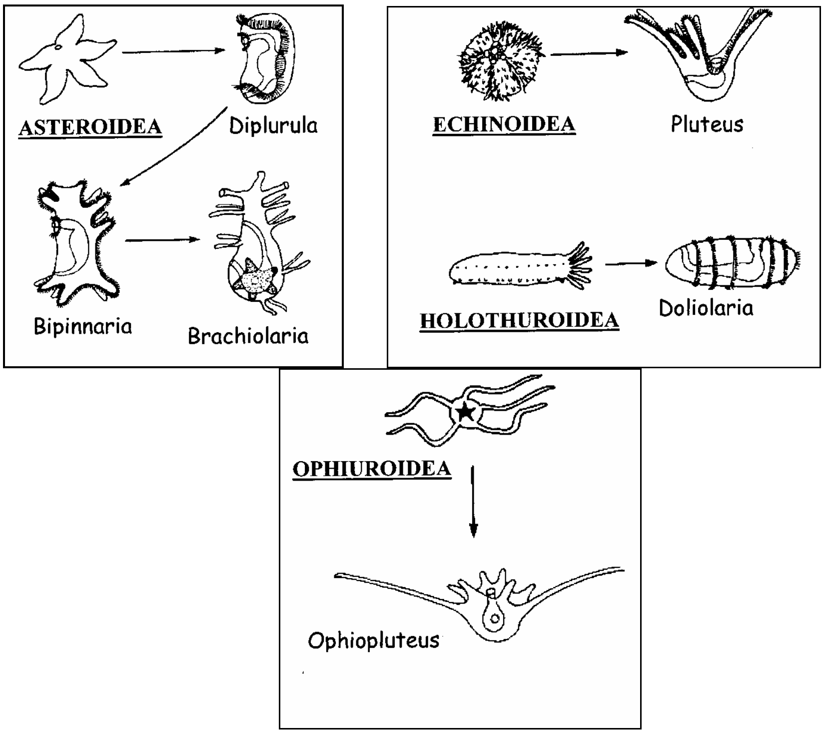

Fig. 15.6. Life histories and larval types in the different classes of echinoderms (underlined). *Source:* Barnes *et al.* (1989)

3.8.1 Regeneration: Some sea stars are capable of regenerating lost arms and in some cases, lost arms have been observed to regenerate a complete sea star. Sea cucumbers discharge parts of their internal organs when disturbed. The discharged organs and tissues are quickly regenerated. Sea urchins constantly lose their spines through damage and replace them.

3.9 Economic importance of echinoderms

- Studies have demonstrated the significance of the pluteus larva of the sea urchin in the pelagic food chain.
- Many species of sea urchins are exploited in some European countries such as France, Spain or Croatia, due to the high commercial value of their tasty gonads
- Toxicity tests using embryos and larvae of sea urchin in the assessment and monitoring of marine pollution.
- Echinoderms play a major role in marine ecosystems. E.g. grazing sea urchins reduce the rate of colonization of bare rock; burrowing sand dollars and sea cucumbers deplete the

sea floor of nutrients and encourage deeper penetration of the sea floor, thus increasing the depth to which oxygenation occurs.

- ☞ Starfish and brittle stars prevent the growth of algal mats on coral reefs, which would obstruct the filter-feeding constituent organisms.
- ☞ Some sea urchins can bore into solid rock, eroding rock faces which release nutrients into the ocean.
- ☞ The echinoderms are also the staple diet of many organisms, most notably the otter
- ☞ Many sea cucumbers provide a habitat for parasites, and also crabs, worms and snails.
- ☞ The extinction of large quantities of echinoderms appears to have caused a subsequent overrunning of ecosystems by seaweed, or the destruction of an entire reef.
- ☞ The fine spines of certain species of sea urchins pierce human flesh, and may break off when an attempt is made to remove it.
- ☞ Sea cucumbers are also considered a delicacy in some countries of south East Asia. They are well known as *bêche de mer* or *Trepang* in China and Indonesia. The sea cucumbers are dried, and the potentially poisonous entrails removed.
- ☞ The strong poisons of the sea cucumbers are often psychoactive but their effects are not well understood. It appears that some sea cucumber toxins restrain the growth rate of tumor cells, which has sparked interest from cancer researchers.
- ☞ The calcareous tests or shells of echinoderms are used as a source of lime by farmers in areas where limestone is unavailable. The trade in the shells is often carried out in conjunction with shellfish farmers, for whom the starfish pose a major irritation by eating their stocks.

4.0 Conclusion

Echinoderms are spiny skinned, coelomate, deuterostome, marine invertebrates.

5.0 Summary

- Echinoderms are bilaterally symmetrical as larvae and radially symmetrical as adults.
- Various calcareous structures form an internal skeleton.
- Part of their coelom forms a water vascular system that serves the tube feet.
- Their pentaradial symmetry and water vascular system are two of their very unique attributes. They are deuterostomes and therefore linked to the chordates.
- They are dioecious and have various larval forms.
- There are three subphyla and six classes of echinoderms.
- Importance of Echinoderms is limited.

6.0 Tutor Marked Assignment

1) How are the echinoderms and the chordates related?
2) What do you understand by pentaradial symmetry?
3) What is the madreporite?
4) Give one **very unique** feature of the echinoderms.
5) How many subphyla of the Echinodermata are currently recognized?
6) List the classes of the subphyla of echinoderms.

7.0 References/Further Reading

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