Indira Gandhi National Open University
School of Sciences

BGYCT-137
STRATIGRAPHY AND PALAEONTOLOGY

Block

4

INVERTEBRATE PALAEONTOLOGY

Course Design Committee

Prof. Vijayshri
Former Director
School of Sciences
IGNOU, New Delhi

Prof. V. K. Verma (Retd.)
Department of Geology
University of Delhi,
Delhi

Late Prof. Pramendra Dev
School of Studies in Earth Sciences
Vikram University
Ujjain, MP

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Hyderabad

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School of Sciences, IGNOU

Prof. Meenal Mishra

Prof. Benidhar Deshmukh

Dr. M. Prashanth

Dr. Kakoli Gogoi

Dr. Omkar Verma

Block Preparation Team

Course Contributor
Dr. Omkar Verma (Units 13, 14, 15 & 16)
School of Sciences
IGNOU, New Delhi

Content Editor
Prof. (Retd.) S. K. Shah
Department of Geology
University of Jammu
Jammu

Language Editor
Dr. Kishor Kumar
Wadia Institute of Himalayan Geology
Dehra Dun

Transformation: Dr. Omkar Verma
Course Coordinators: Dr. Omkar Verma and Dr. Kakoli Gogoi

Audio Visual Materials

Dr. Amitosh Dubey
Producer, EMPC, IGNOU

Dr. Omkar Verma
Content Coordinator

Production

Mr. Rajiv Girdhar
A.R. (P), MPDD, IGNOU

Mr. Sunil Kumar
A.R. (P), SOS, IGNOU

Mr. Hemant Kumar
S.O. (P), MPDD, IGNOU

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BLOCK 4: INVERTEBRATE PALAEONTOLOGY

In Block 3, you have been introduced to fossils, their major groups and evolution of life. Fossils are the remains of the past life, which are commonly preserved in the sedimentary rocks. Earliest fossil record shows that life existed about 3800 million years (Myr) before the present. Life on Earth comprises six kingdoms, which are Eubacteria, Archaea or Archaeobacteria, Protista, Fungi, Plantae and Animalia. Sometime, the kingdoms Eubacteria and Archaea are grouped together under a single kingdom known as Monera. Animals are, further divided into two major groups such as invertebrates and vertebrates. The fossil record also reveals that invertebrates appeared much earlier than vertebrates on the planet Earth. Invertebrates are animals without backbones or vertebral column. They are a wondrously diverse group of animals with a fossil record spanning over 600 Myr before the present. The abundance, diversity and wide range of habitats of invertebrate fossils make them an ideal resource for palaeontologists to use in learning the geological history of Earth.

There are more than 20 phyla of invertebrates and among them the sponges, cnidarians, bryozoans, brachiopods, molluscs, echinoderms, sarcodina and arthropods are the major phyla, which are readily preserved as fossils and are available to the palaeontologists for study. The study of invertebrate fossils reveals that they probably evolved from metazoan (multi-cellular organisms) ancestors during the late Precambrian around 600 Ma ago. In fact, these are animals that lived in a variety of environments including marine, freshwater and terrestrial. Invertebrate fossils are very useful for learning the geology of our planet. They also provide a unique window into the past and allow us to know how life has responded to various environmental conditions throughout the Earth's history and help us to reconstruct the history of life and environment of the past.

This block deals with invertebrate fossils. In this block, you will be introduced to the systematics, morphology and geological history of major groups of invertebrates such as corals, brachiopods, molluscs, trilobites and echinoderms. It may be mentioned here that without having an adequate knowledge of the anatomy of soft parts of invertebrates; it would be difficult to understand the morphology of the hard parts. Taking this into consideration, an appropriate attention is also given to describing the more important soft parts of invertebrates. An attempt has also been made to provide best illustrations wherever required so that you will get proper understanding of the morphology of invertebrates.

This block, comprising four units, deals with five groups of invertebrates.

Unit 13 deals with main groups of brachiopods and corals. It gives a general introduction and describes taxonomy, morphology and geological history of brachiopods and corals. It emphasises the paleontological significance of corals and *Lingula*, which is a living fossil of Brachiopoda.

Unit 14 deals with the general introduction, taxonomy, morphology and geological history of two main classes of molluscs: Bivalvia and Gastropoda. It explains the fundamental organisation and classification of molluscs in general. The major differences between bivalves and brachiopods are also discussed in this unit.

Unit 15 deals with the general introduction, taxonomy, morphology and geological history of cephalopod molluscs. Cephalopoda represents the third and the largest class of Mollusca. This unit describes the two principal groups of cephalopods, which are nautiloids and ammonoids. In addition, it discusses the differences between nautiloids and ammonoids and the functional adaptations in ammonoids.

Unit 16 introduces the taxonomy, morphology and geological history of trilobites and echinoderms. It focuses on the two major groups of echinoderms, namely, crinoids and echinoids.

Expected Learning Outcomes

After studying this block, you should be able to:

- define main fossil groups of invertebrates such as corals, brachiopods, molluscs, trilobites and echinoderms;
- classify the major groups of invertebrates;
- describe their systematics and morphology; and
- discuss their geological distribution.

We wish you all success in this endeavour!

UNIT 13

BRACHIOPODS AND CORALS

Structure

13.1 INTRODUCTION

Almost all the major groups of invertebrates including those living today appeared in the fossil record near the end of early Cambrian period around 514 million years (Myr) ago. The Cambrian or early Palaeozoic life was largely confined to the marine realm in which brachiopods and corals were the two major components in addition to some others. Hence, it is true to say that life the history of these groups of invertebrates is considerably long, about 514 Myr old. Brachiopods and corals are marine animals. Today both these groups have decreased in numbers compared to Palaeozoic times. You can see the living brachiopods at a few beaches and corals in shallow tropical waters. In this unit, we will discuss the systematics, morphology and geological history of brachiopods and corals.

Expected Learning Outcomes

After reading this unit, you should be able to:

- ❖ define brachiopods and corals;
- ❖ describe the morphology of brachiopod shell or valves and coral skeleton;
- ❖ discuss the geological history of brachiopods and corals;
- ❖ list the major groups of brachiopods and corals; and
- ❖ analyse the significance of coral growth rings.

13.2 BRACHIOPODS

The Brachiopoda (Brack-i-oh-poda) is a major fossil group of animals. Though present day brachiopods are an insignificant group, they have a long fossil history and at one time they were a dominant and diverse phylum of invertebrate animals. They are entirely marine animals with bilateral symmetry and having a soft coiled ciliated feeding and respiratory organ known as **lophophore**, which is present within a two-valved shell. Brachiopods occur in all oceans at depths ranging from the intertidal to 5000 m. Most brachiopods live on the bottom of the ocean floor, though some burrow. Till date no brachiopod has been found in the fresh water environment.

13.2.1 What Is Brachiopoda?

Brachiopoda is an independent phylum of invertebrates. The name Brachiopoda is derived from Latin words **brachium** meaning **arm** and **poda** meaning **foot**, which gave its name to the phylum (literally arm-foot). Brachiopods are commonly known as **lamp shells**, because these shells have some resemblance to Roman oil lamps. All brachiopods are sessile (non-mobile), benthic, solitary marine animals having shells made of two unequal valves and live on the sea floor usually in clusters. Many of them remain fixed to the sea floor while others just lie on the sea-bed. They are filter-feeders and collect their food particles from ocean currents by using the lophophore. They have been found living in a wide range of marine environments from shallow marine to deep marine and warm tropical waters to cold Antarctic seas. The presence of brachiopod fossils in sedimentary rocks indicates ancient marine conditions.

The brachiopod shells are made up of mineral calcite ($CaCO_3$ - Calcium Carbonate). They consist of two unequal valves that enclose its soft body's tissues such as mantle, lophophore, pedicle and muscles. The two valves vary in size and morphology and are joined together in two different ways either by hinge (teeth and sockets) or by muscles (Fig. 13.1). Based on the nature of joining two valves, the brachiopods were previously grouped into two classes, namely, **Articulata** and **Inarticulata**. In articulate brachiopods, the two valves are joined by means of teeth and sockets and in inarticulate brachiopods, they are held together by muscles only. Presently, brachiopods are divided into three classes: Linguliformea, Craniiformea and Rhynchonelliformea based on cladistic analyses. However, linguliformeans and craniiformeans represent inarticulate brachiopods and rhynchonelliformeans refer to articulate brachiopods (Benton and Harper, 2009; Milsom and Rigby, 2010).

Fig. 13.1: Shells of brachiopods.

Brachiopods have some superficial similarity to bivalves in that the shell of both animals is made of two valves. The fundamental difference between these two groups of animals is in the size and position of the valves. In brachiopods, the two valves are of unequal size while size of valves is equal in case of bivalves. Moreover, the valves of brachiopods are ventral and dorsal in position (Fig. 13.2) while those of bivalves are right and left. We will discuss bivalves in Unit 14.

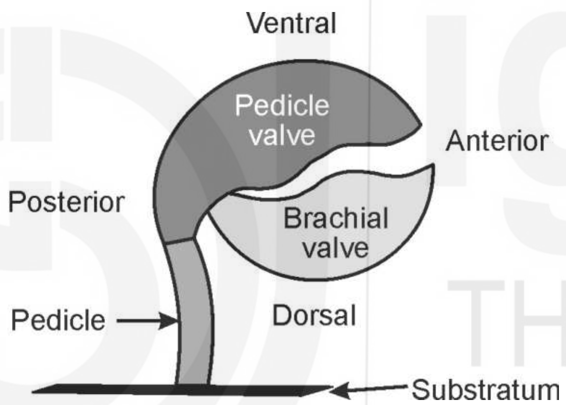

Fig. 13.2: Schematic of a living brachiopod showing the position of pedicle and brachial valves with respect to the soft body parts. The valve that bears the pedicle opening is always known as ventral and the valve that contains the support for the lophophore is dorsal.

13.2.2 Systematic Palaeontology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Brachiopoda
Subphyla	Linguliformea
	Craniiformea
	Rhynchonelliformea

The basic differences between the above mentioned subphyla of brachiopods are listed in Table 13.1.

Did you know: In palaeontology, the term calcareous is used to represent the chemical composition of the shells of organisms e.g., molluscs, which are made up of mainly calcium carbonate. However in geology, the term calcareous is applied to a sediment, sedimentary rock, or soil type which contains a high proportion of calcium carbonate.

Table 13.1: Simplified characteristics of three subphyla of brachiopods.

Characteristics	**Phylum Brachiopoda**		
	Subphylum Linguliformea	**Subphylum Craniiformea**	**Subphylum Rhynchonelliformea**
Shell chemistry	Organo-phosphatic	Calcareous	Calcareous
Valves joining system	Valves are not joined by teeth and socket joining mechanism	Valves are not joined by teeth and socket joining mechanism	Valves are joined by teeth and socket joining mechanism
Pedicle	Present	Reduced or absent	Present

13.2.3 Morphology

The shell of a brachiopod consists of two-valves which are held together either by teeth and socket (e.g., rhynchonelliformeans or articulates) or by muscles (e.g., linguliformeans and craniiformeans or inarticluates). It is important to note that there are certain basic morphological features, which are common in all types of brachiopods. Since articulate brachiopods are well-represented in the fossil records, they are more important from a paleontological point of view than inarticulates. Also they bear all the hard parts that are seen in inarticulates, hence, here we will describe the morphology of articulate brachiopods only.

The two valves of brachiopods are morphologically quite different, especially in terms of size, shape and orientation. However, in typical brachiopods, each valve is bilaterally symmetrical and one valve is always larger than the other. The larger valve is commonly known as **pedicle** or **ventral valve**. It contains an opening known as **pedicle opening** or **foramen** at the beak where a fleshy or muscular stalk called the **pedicle** emerges and attaches the animal to the ocean floor or to another animal. The smaller valve is known as **brachial** or **dorsal valve** (Fig. 13.3). It contains the lophophore (a food gathering organ) along with its supports. Lophophore has two arms called **brachia**, which give the name to the valve.

Each valve has a pointed end which is known as **beak** and it marks the beginning of shell growth. In brachiopod shells, the shell growth mostly occurs in the forms of concentric lines, radial ribs or corrugations on the exterior surface of the valves. The arched part of the valve near the beak is called **umbo** and it is more pronounced on the pedicle valve. The beak is considered the **posterior** end of the valve whereas the rounded margin located opposite to the beak is the **anterior** end as shown in Fig. 13.4.

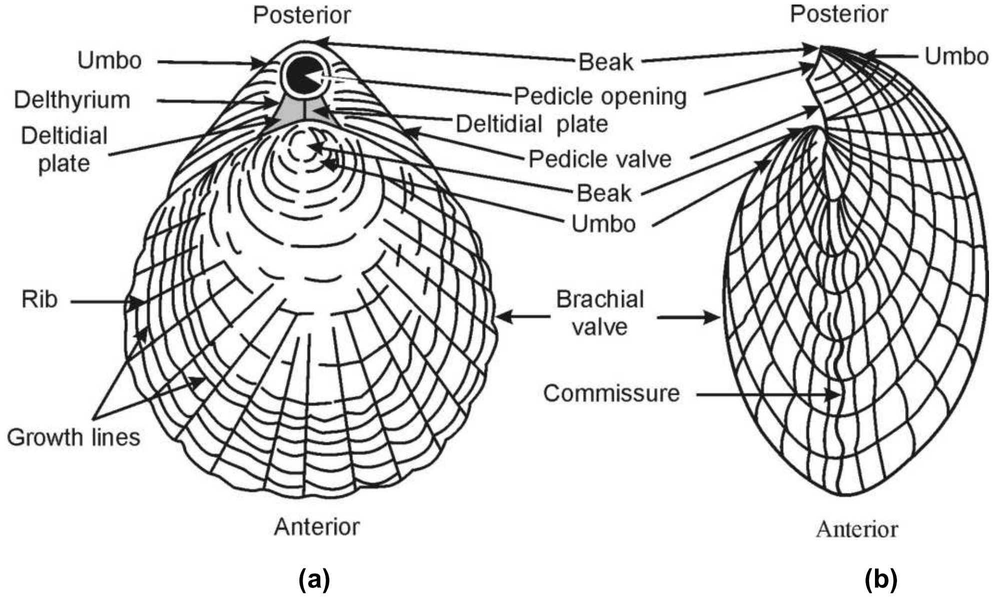

Fig. 13.4: Shells of brachiopods showing external morphology: a) dorsal view; and b) side view.

Commissure is the line where the two valves meet (Fig. 13.4b). It may be straight or zig-zag. Brachiopods have muscles that are used to open and close their valves. They are attached inside the valves and their places of attachment are marked by smooth, depressed or elevated areas which are described as **muscle scars** or **markings**. In articulate brachiopods, the opening and closing of the valves are controlled by two sets of muscles, namely, the diductor and adductor muscle scars. The **diductor muscle scars** open the valves while **adductor muscle scars** close the valves (Fig. 13.5). There is another set of muscle scars that are present on the pedicle valve known as **adjustor muscle scars**. In living conditions, a set of adjustor muscles are attached here and on the other side they are attached to pedicle to facilitate the movement of pedicle.

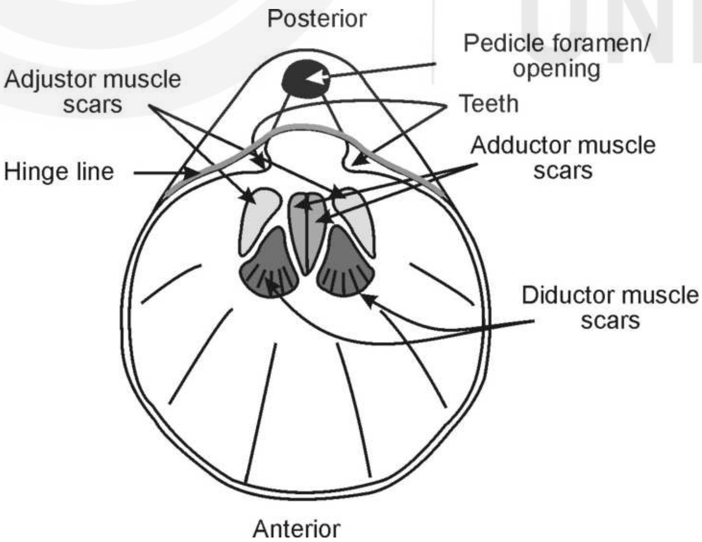

Fig. 13.5: Dorsal view of a brachiopod shell showing internal morphology of pedicle valve. (Source: simplified after Clarkson, 1979)

In some brachiopods, the pedicle valve has a deep medial depressed area described as the **sulcus** that receives a medial elevated portion termed as **fold** of the brachial valve. T**eeth** are knob-like projections that are present on the posterior end of the pedicle valve and fit into the small depressions known as **sockets** of the brachial valve. The contact point where teeth and sockets of the two valves rotate to open and close forms the **hinge** and the portion of the posterior end where both valves meet is known as **hinge line** (Fig. 13.5). A straight hinge line is described as **strophic,** while a curved one is named as **astrophic**.

The flat or curved surface between the beak and hinge line is called the **interarea**, which may be present on both the valves. Interarea of pedicle and brachial valves are commonly known as the **pedical interarea** and **brachial interarea**, respectively. An interarea is more conspicuous on the pedicle valve. Directly beneath the beak, the interarea of the pedicle valve may be interrupted by a triangular cavity called **delthyrium** from which emerges the pedicle. The corresponding cavity in the brachial valve is known as **notothyrium** as shown in Fig. 13.6. The delthyrium may be partly or fully closed by the two calcareous **deltidial plates** forming the **deltidium** and the corresponding covering of notothyrium is known as **chilidium** (Moore et al., 1997).

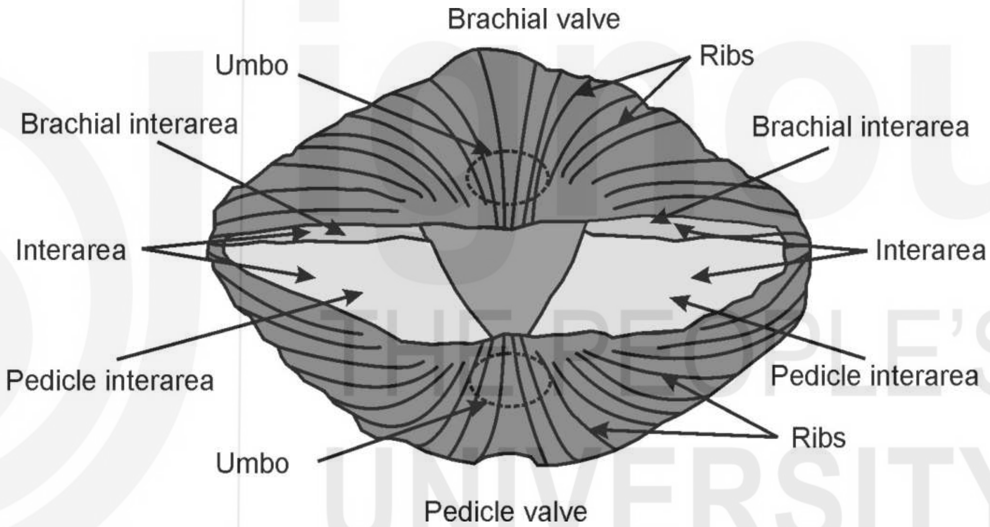

Fig. 13.6: Posterior view of a brachiopod shell showing external morphology.

In the delthyrium area, the single calcareous plate covering is termed as deltidial plate and if the same area has more than one plate then it is termed as deltidium. Single calcareous plate covering of notothyrium is known as chilidial plate and two or more plates covering is described as chilidium.

The shell of most articulate brachiopods consists of two layers; an outer layer made of organic compounds **periostracum**, and mineralised (inorganic) inner layers referred to as **primary** and **secondary**. Brachiopod valves come in a variety of shapes like convex, concave or flat and some forms show interesting external ornamentation of costae and plicae. **Costae** are very fine radial ridges on the external surface of the valve originating from the beak and **plicae** are radial ridges present on external as well as internal surfaces of the valve. In a few forms, the valves are covered with spines.

Key morphological features of brachiopods: pedicle (ventral) valve, brachial (dorsal) valve, beak, umbo, commissure, teeth, sockets, hinge line and interarea.

SAQ 1

a) What is the function of a lophophore in brachiopods?

b) Name the three subphyla of Brachiopoda.

c) Match the following:

(i) Inarticulate brachiopods	(a) Brachiopods with teeth and sockets
(ii) Pedicle valve bears	(b) Posterior end where valves meet
(iii) Hinge line	(c) Brachiopods without teeth
(iv) Articulate brachiopods	(d) Brachiopod valves
(v) Unequal valves with a bilateral symmetry	(e) Pedicle opening

13.2.4 Geological History

Brachiopods have a very long geological history because they first appeared near the beginning of the Cambrian period and some of the forms are still alive today on the floor of the modern oceans (Fig. 13.7). Most of the Cambrian brachiopods were considered to be inarticulates, but few forms of primitive articulate brachiopods are also known from Cambrian. They diversified in the Ordovician and reached the peak of their diversity during the Ordovician, Silurian and Devonian. Cambrian faunas were dominated by the inarticulate and Ordovician by articulate brachiopods. They remained a dominant community in the marine ecosystem throughout the Palaeozoic era. At the end of Palaeozoic, many brachiopod families became extinct, and only a very few of them made the transition to the post-Palaeozoic (i.e. Mesozoic and Cenozoic) time. Only a few orders of brachiopods such as Lingulida, Discinida, Craniida, Rhynchonellida, Thecideida and Terebratulida have living representatives today. Because of their great diversity, they have been used as index fossils for dating the Palaeozoic rocks. The geological range of some of the orders of brachiopods is given in Table 13.2.

Table 13.2: Geological range of some orders of brachiopods.

Subphylum	Order	Geological range	Important genera
Linguliformea	Lingulida	Cambrian to Recent	*Lingula, Obolus, Pseudolingula*
Craniiformea	Craniida	Ordovician to Recent	*Crania, Neocrania*
Rhynchonelliformea	Obolellida	Cambrian	*Obolella, Trematobolus*
	Strophomenida	Ordovician to Triassic	*Billingsella, Eoplectodonta*
	Productida	Ordovician to Triassic	*Productus, Gigantoproductus*
	Orthida	Cambrian to Permian	*Orthis, Dalmanella*
	Pentamerida	Cambrian to	*Pentamerus,*

		Devonian	*Stricklandia*
	Rhynchonellida	Ordovician to Recent	*Rhynchonella, Wilsonia*
	Spiriferida	Ordovician to Permian	*Spirifer, Mucrospirifer*
	Spiriferinida	Carboniferous to Jurassic	*Spiriferina, Punctospirifer*
	Terebeatulida	Devonian to Recent	*Terebratella, Magellania*

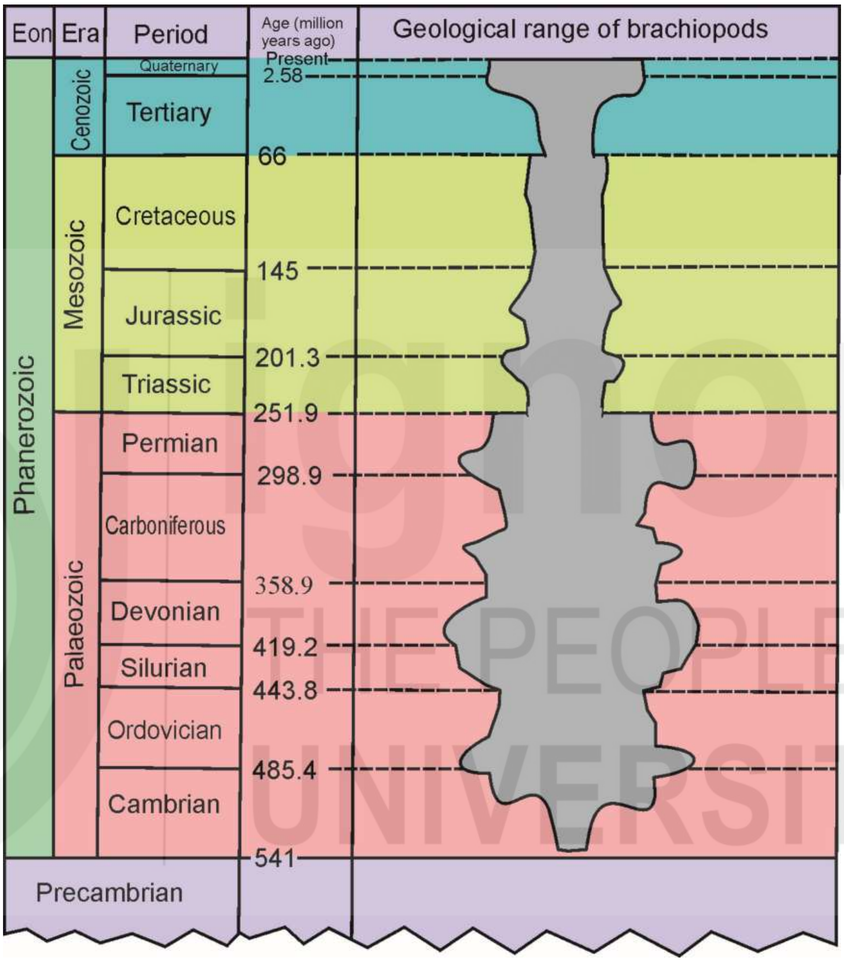

Fig. 13.7: Stratigraphic distribution of brachiopods. Width of column represents the abundance or diversity of brachiopods in a particular period/era.

The brachiopods faced five major events of extinction which were followed by events of recoveries and diversifications. These events are end-Ordovician, late Devonian, end-Permian, end-Triassic and end-Cretaceous mass extinctions. Out of these, three events, namely, end-Ordovician, end-Permian and end-Cretaceous were very severe events which caused about 80%, more than 90% and around 70%, extinction among brachiopods at family and species levels, respectively. As a result of such extinction events, out of 4500 fossil genera of brachiopods, only 120 are living today while all others are extinct.

Story of *Lingula* – As a Living Fossil

Lingula is the best known representative of linguliformean (inarticulate) brachiopods and belongs to the class Lingulata. It first appeared in the

Cambrian and is still persisting today. Thus *Lingula* has a long geological history, ranging from Cambrian to Recent (i.e., more than 550 million years) and its body shows morphological stability, meaning no significant changes took place in the biology of *Lingula* during its entire span of life history. Since *Lingula* has survived today without any significant morphological changes from the early Palaeozoic, it is often considered as one of the classic examples of **living fossils**. It is important to note that *Lingula* has escaped every major extinction event throughout history.

SAQ 2

a) What is the geological range of brachiopods?

b) Which of the following brachiopods appeared first in the fossil record?

i) Inarticulate brachiopods ii) Articulate brachiopods

c) Which of the following era is also known as age of brachiopods?

(i) Mesozoic (ii) Palaeozoic (iii) Cenozoic

d) *Lingula* belongs to the order:

(i) Lingulida (ii) Rhynchonellida (iii) Spiriferida

13.3 CORALS

Corals are cnidarians (Ni-da´-ri-ans). Apart from corals, phylum Cnidaria also includes anemones, jellyfish, sea fans, sea pens and their close relatives. Most cnidarians live in the seas, but a few thrive in the fresh water environment. Cnidarians are characterised by their cylindrical body, radial symmetry and carnivorous nature. They have two basic life forms, namely, polyp and medusa (Fig. 13.8). **Polyps** are usually sessile animals, which have a tube-shaped body with an opening at the top that functions both as a mouth and anus. This opening is surrounded by a number of tentacles. Typical examples of polyps are corals and sea anemones. While **medusae** (singular medusa) are free-swimming sea inhabitants and their body has an inverted orientation relative to that of polyps. The mouth of a medusa is located downward. The jellyfish is a common example of medusa. Since the tentacles of cnidarians have poisonous stinging cells, they are also known as "**nettle-bearers**" (Benton and Harper, 2009).

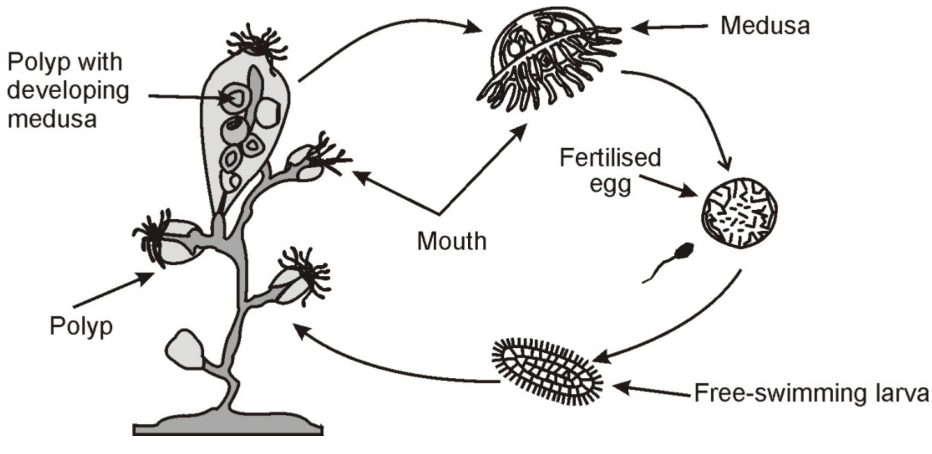

Fig. 13.8: Life cycle of cnidarians showing polyp and medusa forms. Note that polyp is attached to the bottom/substratum and has its mouth upward. Medusa is a floating form of cnidarians having its mouth downward. (Source: simplified after Clarkson, 1979; Benton and Harper, 2009)

13.3.1 What are Corals?

Corals are flower-like simple sea animals (Fig. 13.9a). They are composed of tiny, fragile animals known as **coral polyps.** They have no medusa forms. Corals occur mostly in the form of colonies (groups of thousands of coral polyps) (Fig. 13.9b), and very few corals are solitary (Fig. 13.9c). The size of an individual coral ranges from tiny up to 30 cm in diameter. Coral polyps are nocturnal; as a consequence, they remain inside their skeletons during the day. At night, polyps extend their tentacles to feed by capturing and eating planktons. Some coral polyps, for example, polyps of scleractinian corals have established a symbiotic relationship with an important group of photosynthetic algae known as **zooxanthellae**. Zooxanthellae give brilliant colour to the corals and keep them healthy by providing them nutrition and removing their waste.

(a) (b) (c)

Fig. 13.9: Corals: a) Living; b) Colonial; and c) Solitary corals. (Courtesy: Prof. G.V.R. Prasad for b and c)

Corals are classified into two types: hard corals and soft corals.

i) **Hard Corals**: They have a hard exo-skeleton made of calcium carbonate (limestone). Hard coral polyps extract calcium from the sea water and use it to create a hardened structure for protection and growth. They are also known as the **stony** and **reef building corals**.

ii) **Soft Corals**: They have no exo-skeleton; hence they are more tree-like and flexible. The skeleton of soft coral is located within their bodies and is less rigid than the skeleton of hard corals.

To survive and grow, corals require shallow, clean, mud/sediment free water where sunlight can reach. They thrive in water having 5 to 10 m depth, however, some corals can grow poorly at depths of 90 m. Hard corals grow best in warm water (tropical oceans) having temperature in the range of 21 - 29°C whereas soft corals thrive mainly in cold, high-latitude waters (Garrison, 2009). Corals prefer salt water to survive, so this is the reason that they do not thrive in areas where rivers drain fresh water into the ocean.

13.3.2 Systematic Palaeontology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Cnidaria
Class	Anthozoa (corals and sea anemones)

Corals belong to the class Anthozoa. Anthozoans include two groups of corals as discussed above, namely, soft corals and hard corals. Soft corals (subclass Octocorallia), have a poor fossil record because of their soft skeleton, but they are well known in modern oceans and are represented by the sea pens and sea fans. Hard corals (subclass Zoantharia) have left a good fossil record due to the easy preservation of their skeletons. Hence, palaeontologists are more concerned with the hard corals. Zoantharians comprise three orders: Rugosa, Tabulata and Scleractinia. Of these, rugose and tabulate corals are extinct and all modern corals are scleractinian corals.

13.3.3 Morphology

Coral skeletons are calcareous, which can be made either by calcite or aragonite (both are mineral forms of calcium carbonate – $CaCo_3$). As you know polyp is an individual coral animal and it has a soft body that secretes a cup-shaped skeleton in which the animal sits. The whole skeleton of a simple coral is known as the **corallum** (Fig. 13.10). In case of the colonial corals, the skeleton of each individual coral of the colony is described as a **corallite**. The skeleton of a simple coral is more or less conical or horn-like in shape. The shape of the colonial corals tends to be dome-like. The bowl-shaped depression at the distal end of the corallum which contains soft parts of the animal is termed as **calyx** (plural **calices)**. The outermost calcareous wall of the skeleton which forms the boundary of corallum and sometimes shows growth rings is called **epitheca** (Fig. 13.10).

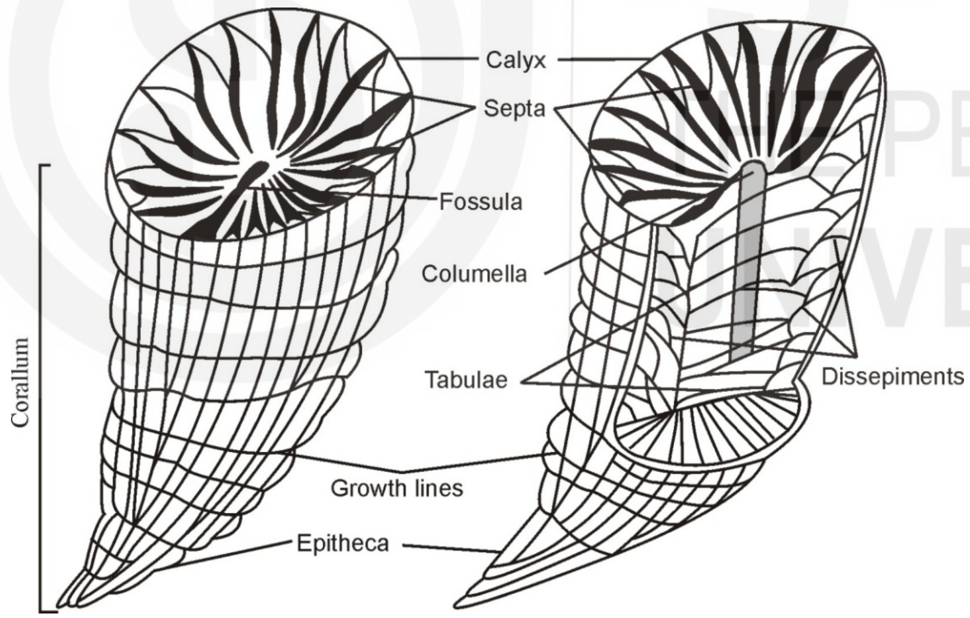

Fig. 13.10: Line drawings of corals showing morphological features. (source: redrawn after Nield and Tucker, 1985; Milsom and Rigby, 2010)

A number of vertical and horizontal structures are developed within the corallum to support the growth of the polyp. The vertical structures/plates radiating from the centre of the cavity within the corallum are termed as **septa** (singular septum). Thin plates joining the adjacent septa are the **dissepiments**. The septa may vary in size. As the polyp grows more septa are required to adjust the growth of the skeleton. The first formed septa known as **prosepta** (primary septa), which are longer and thicker than the secondary septa, **metasepta** intercalated between them (Fig. 13.11). Sometimes, the septa appear outside the corallum as ridge-like structures called **costae**. The horizontal structures/plates are known as **tabulae** (singular tabula).

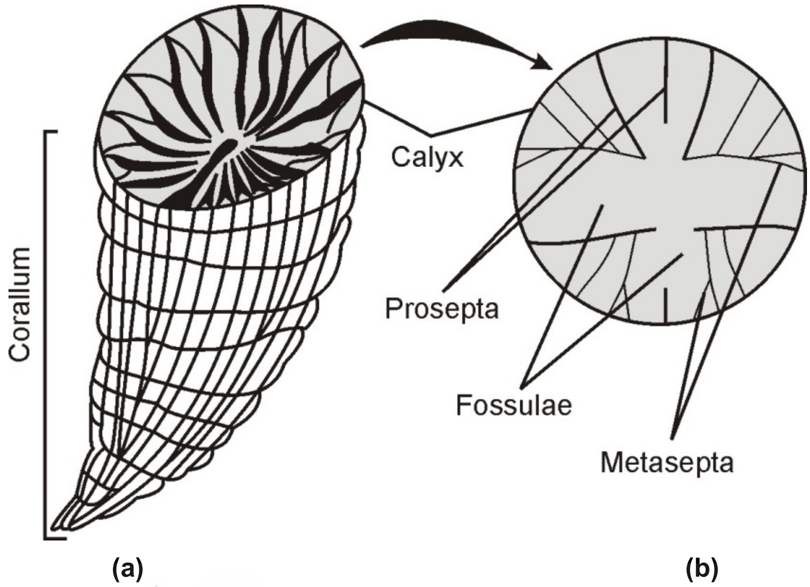

Fig. 13.11: Line drawing showing coral morphology: a) coral skeleton; b) enlarged view of calyx (a) showing prosepta and metasepta.

Fossula is a pit/depression at the surface of the calyx which forms due to the stoppage of growth of septa. **Columella** is a vertical rod which occupies the central region of the coral and extends from the base of the coral's chamber at the bottom of the calyx (Fig. 13.10). A solid structure of columella with knob or pointed end at the calyx is said to be **styliform**.

Key morphological features of corals: corallum, corallite, calyx, epitheca, septa, dissepiments, prosepta, metsepta, costae, tabula, fossula, columella and styliform.

Some corals do not form colonies and remain simple or single throughout life. While other corals which are simple in their young stage form communities during the later stage by giving off buds. Such corals are called **reef building** corals. The budding process involves a loss of individuality and transforms a simple coral polyp into a compound individual, which gives rise to a mass of polyps known as a **colony**. Therefore, it is not necessarily true that all corals possess all above described morphological characters. Now let us familiarise ourselves with the three groups (orders) of the hard corals in brief.

i) **Tabulate Corals (Order Tabulata)**: They are colonial corals and their skeletons are made of calcite. They have very well developed tabulae and weakly developed septa (Fig. 13.12a).

ii) **Rugose Corals (Order Rugosa)**: They are solitary and colonial corals and their skeletons are made of calcite. They have well-developed septa and possess coarse ridges on the outer wall of corallum known as **rugae**. The rugae are the rough ridges or wrinkles (rugae) present on the outer surface of the rugose coral Tabulae and dissepiments are common elements of rugose corals (Fig. 13.12b).

iii) **Scleractinian Corals (Order Scleractinia)**: They are solitary and colonial corals. They have light and porous skeletons made of aragonite. They differ from the rugose corals by their patterns of septal insertion. The septal insertion in the scleractinian corals are arranged in sets or multiples of six and in sets of four in case of rugose corals (Fig. 13.12c).

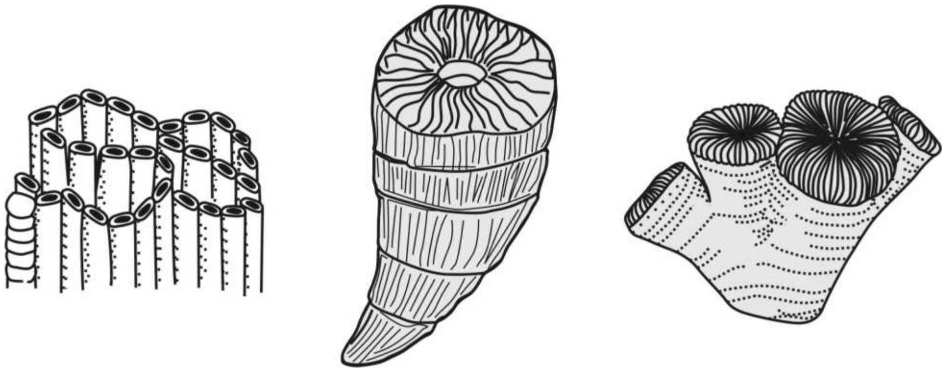

Fig. 13.12: Groups of corals: a) Tabulate; b) Rugose; and c) Scleractinian corals.

13.3.4 Geological History

In the preceding sections of the unit, you have learnt about the general morphology of a coral and about the three orders of hard corals. In this section, we will discuss the geological history of hard corals (Fig. 13.13).

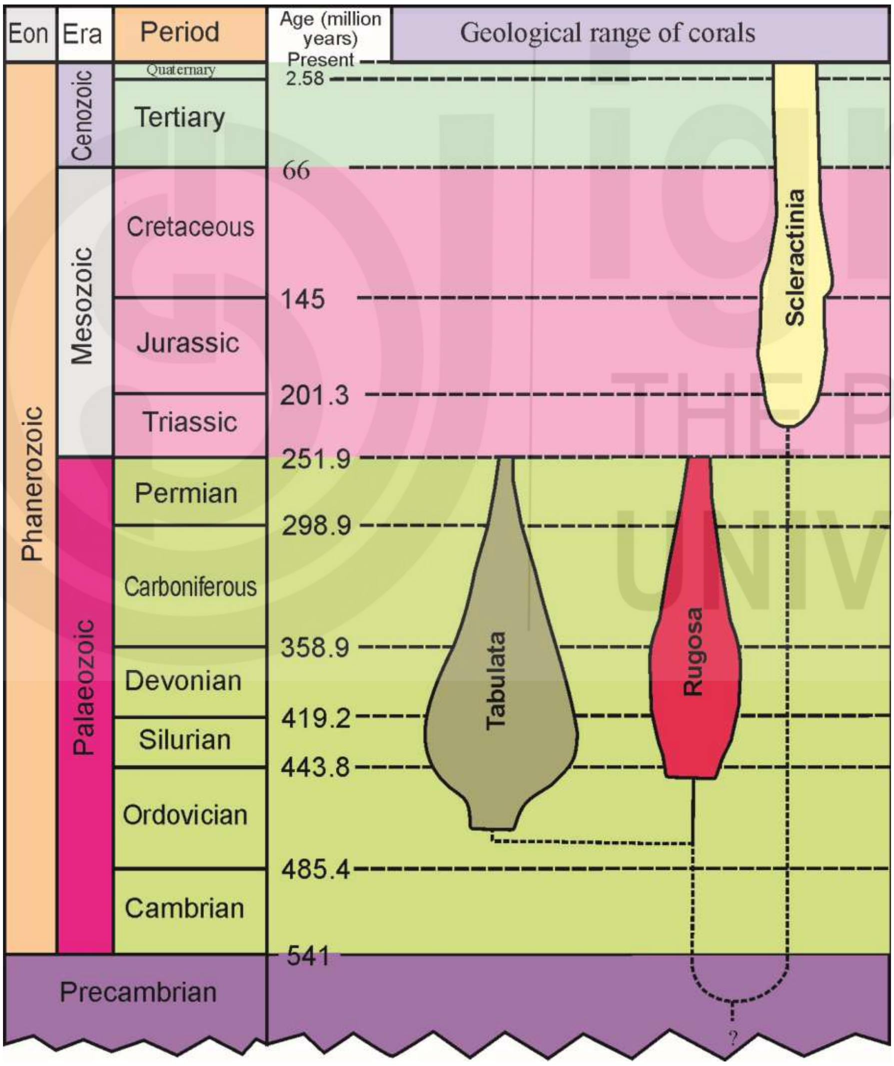

Fig. 13.13: Stratigraphic distribution of three orders of corals. Inferred evolutionary relationships are shown by thin dotted lines. Each group of corals evolved separately possibly from a soft-bodied ancestor. Thickness of the columns shows the abundance of the particular order of corals in a specific period (source: redrawn and modified after Milsom and Rigby, 2010; Jones, 2011). Width of column represents the abundance of corals in a particular period/era.

As you know, corals belong to phylum Cnidaria. Cnidarians first appeared in the Precambrian and there are some doubtful tabulate corals which are known from the Cambrian period. We mentioned earlier that rugose, tabulate and scleractinian are the important fossil coral groups because they have long and well-preserved fossil record. Rugose and tabulate corals evolved in the Ordovician period from soft-bodied anemone ancestors. They are also known as **corals of Palaeozoic era**. They appeared in the Late Ordovician period, diversified in the Silurian, Devonian and declined in the Late Devonian and Carboniferous, and finally became extinct at the end of the Permian period (Fig. 13.13). Scleractinian corals evolved in the middle Triassic from soft-bodied ancestors. They first appeared in the Triassic period and diversified throughout the Mesozoic. However, some representatives or genera of scleractinians became extinct at the Cretaceous/Tertiary boundary, but others radiated rapidly after the Cretaceous/Tertiary boundary mass extinction at around 66 Ma ago (Fig. 13.13). They are also known as **modern reef building corals** and **corals of Meso-Cenozoic era**.

SAQ 3

a) Corals belong to class ………………… .

b) Is medusa present in the corals? Yes or No.

c) Corals are ……………….. (Sea animals or Sea plants).

d) Which group of corals form coral reefs? (a) Octocorallia, (b) Zoantharia.

e) Match the following:

(i) Calyx	(a) Rugose and tabulate corals
(ii) Corallum	(b) Outer wall of coral's skeleton
(iii) Epitheca	(c) Skeleton of a simple coral
(iv) Septa	(d) Horizontal plates present in the body of corals.
(v) Tabulae	(e) Scleractinian corals
(vi) Columella	(f) Bowl-shaped depression at the top of corallum
(vii) Palaeozoic corals	(g) Vertical plates radiating from the centre of the cavity within the corallum
(viii) Meso-Cenozoic coral	(h) Vertical rod occupies the central portion of corals

13.4 CORAL AND EARTH'S ROTATION

You have already learnt about epitheca is the outer wall of the corallite or corallum. In some corals, epitheca shows the development of growth rings or incremental lines. These rings or lines are similar to the tree rings. Let us discuss how corals develop the growth rings in their skeleton. The corals grow by extracting calcium carbonate ($CaCO_3$) from the sea waters and using it to make their skeletons. The density of the coral skeleton varies according to their diurnal, monthly or yearly response to the lunar orbit and environmental conditions, for example, light, weather and temperature. Coral skeletons formed in different conditions have different densities. This creates growth rings on the coral which may reflect daily, monthly or yearly growth increments.

The growth rings are clearly visible in the well-preserved specimens of corals. Commonly, a fossil coral displays three types of growth bandings: fine, thick and widely spaced that reflect daily, monthly and yearly growth cycles, respectively.

Scientists have been studying these rings present in fossil corals to know whether there was any relationship between the development of growth rings in corals and change in the rotation of the Earth. An interesting study to understand this relationship was carried out by John Wells of Cornell University, USA in 1963. Wells worked on Devonian (416 – 359 Myr ago) corals, which had been dated as 370 Myr old using radiometric methods. He calculated the yearly growth bands on a variety of Devonian corals and found that Devonian corals had an average 400 daily growth bands per year. On the basis of these observations, he further suggests that the Devonian year had about 400 days, which means that each day was 21.9 hours long. Another study of corals indicates 390 days per year in the Carboniferous (359 – 229 Myr ago) as compared with approximately 360 days per year in present times. Therefore, based on the coral's growth band study (also known as a coral clock), it has been concluded that the Earth's rate of rotation is decreasing slowly from ancient times due to the gravitation pull of the moon as suggested by astronomical estimates. Hence, coral-clock provides a consistent support to the idea of a decrease in the Earth's rate of rotation which is forwarded based on astronomical and radiometric methods.

13.4 ACTIVITY

Below is a posterior view of a brachiopod shell (Fig. 9.14). Label the following morphological features: pedicle (ventral) valve, brachial (dorsal) valve, beak, umbo, hinge line and ribs.

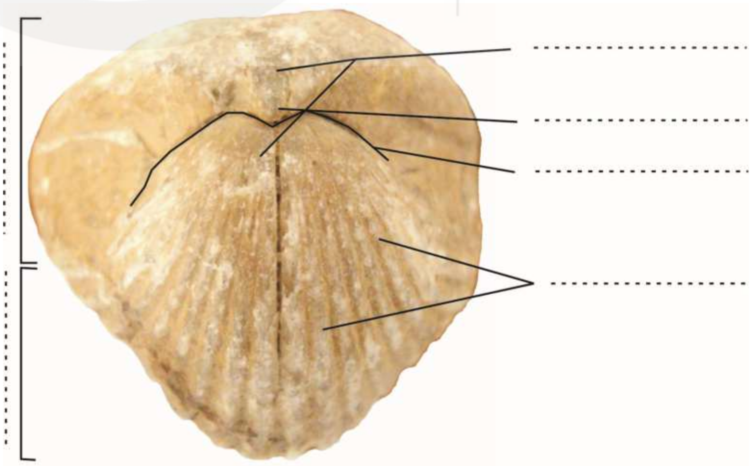

Fig. 9.14: Posterior view of a brachiopod shell.

13.5 SUMMARY

In this unit, you have learnt that:

- Brachiopods and corals are marine invertebrates.

- Pedicle or ventral valve, brachial or dorsal valve, beak, umbo, commissure, teeth, sockets, hinge line and interarea are the morphological features of brachiopod shell.
- Brachiopods are also classified into three groups: Linguliformea, Craniiformea and Rhynchonelliformea. They first appeared in Cambrian and a very few groups are living today. They were more dominant during the Palaeozoic and had experienced five major extinction events.
- Corallum, corallite, calyx, epitheca, septa, dissepiments, prosepta, metsepta, costae, tabula, fossula, columella and styliform are major morphological features of coral skeleton.
- Corals are divided into three groups, namely, Rugosa, Tabulata and Scleractinia. Rugose and tabulate corals were dominant during the Palaeozoic where as scleractinian corals were dominant in Mesozoic and are still living.

13.6 TERMINAL QUESTIONS

1. Discuss the morphology and geological history of brachiopods.
2. Define corals and describe the morphology of coral skeleton.
3. What is stratigraphic range of corals?

13.7 REFERENCES

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13.8 FURTHER/SUGGESTED READINGS

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13.9 ANSWERS

Self Assessment Questions

1 a) Lophophore is soft bodied internal food gathering organ of brachiopods located inside the smaller (brachial) valve of brachiopods. They use it to pump sea water and sieve small food particle from the water.

b) Linguliformea, Craniiformea and Rhynchonelliformea.

c) (i) – (c), (ii) - (e), (iii) - (b), (iv) - (a) and (v) - (d).

2 a) Cambrian to Recent (Present or Holocene)

b) (i) Inarticulate brachiopods

c) (ii) Palaeozoic

d) (i) Lingulida

3 a) Anthozoa

b) No

c) Sea animal

d) (b) Zoantharia

e) (i) - (f), (ii) - (c), (iii) - (b), (iv) - (g), (v) - (d), (vi) - (h), (vii) - (a) and (viii) - (e).

Terminal Questions

1. Refer to section 13.2.
2. Refer to subsection 13.3.1 and 13.3.3.
3. Refer to subsection 13.3.4.

UNIT 14

MOLLUSCS – BIVALVES AND GASTROPODS

Structure

14.1 INTRODUCTION

In Unit 13, you have read about the systematics, morphology and historical distribution of brachiopods and corals. Both are marine animals. Unfortunately, during the course of geological time many forms belonging to these two groups got extinct and, as a consequence, very few of them are surviving in today's oceans.

Now we shall deal with the second largest phylum of invertebrate animals – **Mollusca**. Majority of molluscs are marine animals, but a few of them live in freshwater or are on land. Molluscs canbe divided into four important groups- bivalves, gastropods, cephalopods and chitons. In this unit, we will discuss the basic organisation and classification of molluscs. In addition, we will describe the systematics, morphology and geological history of bivalves and gastropods in detail.

Expected Learning Outcomes

After reading this unit, you should be able to:

- define and classify molluscs;
- outline the organisation and life history of major groups of bivalves and gastropods;
- describe the shell morphology of bivalves and gastropods; and
- discuss the geological history of bivalves and gastropods.

14.2 MOLLUSCS

The Mollusca, widely known as **mollusks**, is the second most diverse and abundant invertebrate phylum after the Arthropoda. Phylum Mollusca contains more than 130,000 living and about 35,000 extinct species that are found as fossils. It includes a wide range of familiar animals such as the oysters, clams and mussels (Bivalvia); snails, slugs, whelks and limpets (Gastropoda); nautiluses, octopuses and cuttlefish (Cephalopoda); chitons (Amphineura) and tooth shells (Scaphopoda).

Molluscs, in general, are unsegmented, soft-bodied animals. The soft body of a typical mollusc is enclosed by an external skeleton secreted by the animal. This external skeleton or shell is known as an **exo-skeleton**. Shell, which is usually composed of calcium carbonate, provides protection from predators as well as support to the animal. Molluscs are mostly marine, but some groups have successfully occupied the fresh water and land habitats. They vary greatly in size: while some are the size of sand grains, a very few forms like squids attain a length of more than16 m. It is interesting to note that molluscs include planktic (floaters), nektic (swimmers) and sessile benthic (bottom dwellers) forms.

Do You Know?

Living molluscs are an important source of food for humans. Some molluscs, especially oysters are cultured to manufacture pearls and their shells are used as ornaments.

14.2.1 Basic Morphology of Molluscs

Molluscs have a remarkable diversity in their body forms and mode of life. Therefore, it could not be possible to explain the basic anatomy of molluscs by choosing any single form. As a result, palaeonologists have developed a hypothetical mollusc of the simplest body plan, which is considered as the probable common ancestor of all molluscs (Fig. 14.1).

If you remove the hard external shell (i.e., exo-skeleton) of a mollusc, then you will find that a mollusc is a soft, elongated and unsegmented animal having a head, a muscular foot, mantle, gill structures and visceral mass. The **head** comprises sensory organs and mouth. It is situated on the anterior side of the shell. **Foot** is a flat sole-like structure which serves as the primary mechanism for locomotion. **Mantle** covers the dorsal and lateral parts of the animal and has a sheet of tissue that secretes the shell. The animal uses **gills** for respiration that are placed posteriorly. The **visceral mass** comprises internal organs for digestion, excretion and circulation.

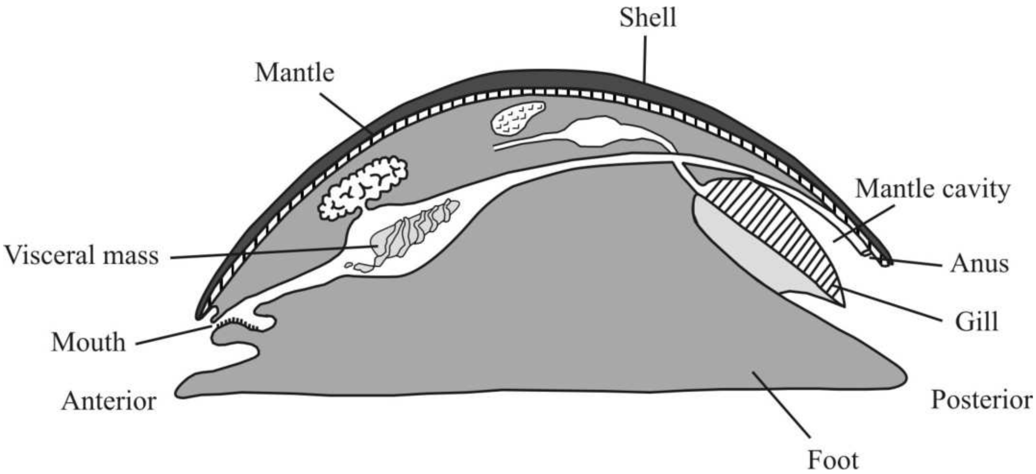


Fig. 14.1: Generalised soft-part morphology of a mollusk. (Source: simplified after Milsom and Rigby, 2010)

The shell is the main hard part of molluscs which is calcareous ($CaCO_3$) in nature. The evolutionary development of molluscs shows that some forms like octopus and squid lost their shell with the passage of time. In other forms, the hard shell remained a major part of the animals, for example, in gastropods, bivalves and ammonoids.

14.2.2 Classification

Phylum Mollusca is divided into five classes, based on the differences in general shell forms and their characteristics, mode of life, nature of foot and certain other soft parts. Here it is significant to note that the nature of shell is considered an important feature in the molluscan classification. The division of classes with characteristic features and age are given in Table 14.1.

Table 14.1: Classification of molluscs. (Source: simplified after Clarkson, 2007; Benton and Harper, 2009)

Classes	Characteristic features
Bivaliva	Two-valved nature of the shell, valves joined along the dorsal hinge line with teeth, sockets and ligament, no head, well-developed foot and gills are modified for respiration and filter feeding. Examples – oysters, mussels and clams. Age – Early Cambrian to Recent.
Gastropoda	Large muscular foot on the ventral side, single valve (i.e., univalve), coiled shell, head is well-developed with eyes and other sense organs. Examples – snails, slugs, whelks and limpets. Age – Late Cambrian to Recent.
Cephalopoda	Advanced intelligent molluscs having well-developed head and sensory organs. Examples – nautiluses, octopuses and cuttlefish. Age – Late Cambrian to Recent.

Amphineura	Shell segmented with eight plates, broad and flat foot and a series of gill pairs. Example – chitons. Age – Late Cambrian to Recent.
Scaphopoda	Shell is long and cylindrical opening at both ends. Example – tooth shell. Age – Devonian to Recent.

Out of all the molluscs, the bivalves, gastropods and cephalopods are significant for geological studies as they are more likely to get preserved as fossils because of the hard nature of their shells. In this unit, we will be discussing the bivalves and gastropods and we will discuss cephalopods in the next unit.

14.3 BIVALVES

Many of you, especially those living near the sea shores are familiar with bivalves because they are the common sea shells that are found on the beach sands. Bivalves form an important and interesting group of molluscs for a number of reasons. Some of which are listed below:

- bivalves represent a wide range of adaptation that is from marine to freshwater and from infaunal burrowers, epifaunal to active swimmers
- they produce valuable by-products such as pearls, which are secreted by the mantle
- living bivalves are an important source of food, and
- wood-boring bivalves damage boats, docks and other wooden structures.

14.3.1 What Is Bivalvia?

Bivalvia is the second largest class of molluscs, which includes cockles, mussels, oysters, clams, shipworms and scallops. Bivalves consist of a twin-valved shell (i.e., shell made up of two almost similar valves) that gives them a superficial resemblance to brachiopods, but varies in shell morphology and symmetry. In many bivalves, the valves are virtually mirror images of each other, but a very few forms like oysters and rudist bivalves have one valve larger than the other. Bivalves have also been described as '**pelecypods**' and '**lamellibranchs**'. However, the term Bivalvia was the first name given to the bivalves and is, therefore, the valid name.

The name Bivalvia was given by Linnaeus in 1758. It is the original name of the Class and is used to describe those animals having shells consisting of two hinged valves, e.g., bivalves. The class Bivalvia has also been referred to by other names such as Pelecypoda and Lamellibranchia. The term Pelecypoda is derived from two Greek words, *Pelekys* meaning a hatchet and *Podos* meaning foot, which signifies a hatchet foot. The name Lamellibranchia is derived from Latin words *Lamella* meaning a small leaf and *Branchia* meaning gills, which signifies the leaf-like form of the gills. Pelecypoda and Lamellibranchia are now considered as out dated class names.

The bivalves are bilaterally symmetrical molluscs in both soft and hard parts, in which the mantle envelops the gills, foot and visceral mass. In addition, the mantle also secretes a calcareous shell which consists of two lateral valves, which are united dorsally. They vary in size from less than 1 mm to 1 m in length, but the majority of them are not more than 10 cm in length.

14.3.2 Systematic Palaeonotology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Mollusca
Class	Bivalvia
Subclass	Palaeotaxodonta
	Cryptodonta
	Pteriomorphia
	Palaeoheterodonta
	Heterodonta
	Anomalodesmata

The class Bivalvia is classified into six subclasses based on certain characteristic features, e.g., dentition, shell microstructure, hinge structure, anatomy of stomach and type of gill.

Common genera of bivalves: *Pecten, Ostrea, Gryphaea, Inoceramus, Trigonia, Cardita, Pinna, Mytilus, Arca, Nucula* and *Alectryonia*.

14.3.3 Morphology

The soft parts such as the mantle, gills and foot of bivalves are covered by a hard exo-skeleton, which is made up of two valves. In most cases, the valves are equal in size, asymmetrical in outline and essentially mirror images of each other. The valves are secreted by the mantle and are made up mostly of calcite ($CaCO_3$), but in few cases valves with aragonite composition are also known.

In bivalves, the two valves are named as **right** and **left** valves (Fig. 14.2), because they are located to the right and left sides of the animal. Each valve has a nose-like pointed apex, which marks the region of initial growth of the shell that is known as **beak**. Beak usually curves toward the anterior (i.e., front) end of valves. **Umbo** (plural **umbones**) is the region of maximum curvature of each valve close to the beak and situated on the dorsal margin of the shell (Fig. 14.2). In most of the bivalves, the two valves are joined together along their dorsal margin by means of elastic ligaments and by an interlocking mechanism of teeth and sockets. The valves open at their ventral margin.

Orientation of the bivalve shell:

If you place the beaks of the shell uppermost in your front, the valve appears on the right side is **right valve** and that on the left is **left valve**. The margin closest to the beak is **anterior** of the shell and opposite margin is **posterior**.

The margin of the shell near the hinge is **dorsal** and the opposite margin is **ventral** (Fig. 14.2).

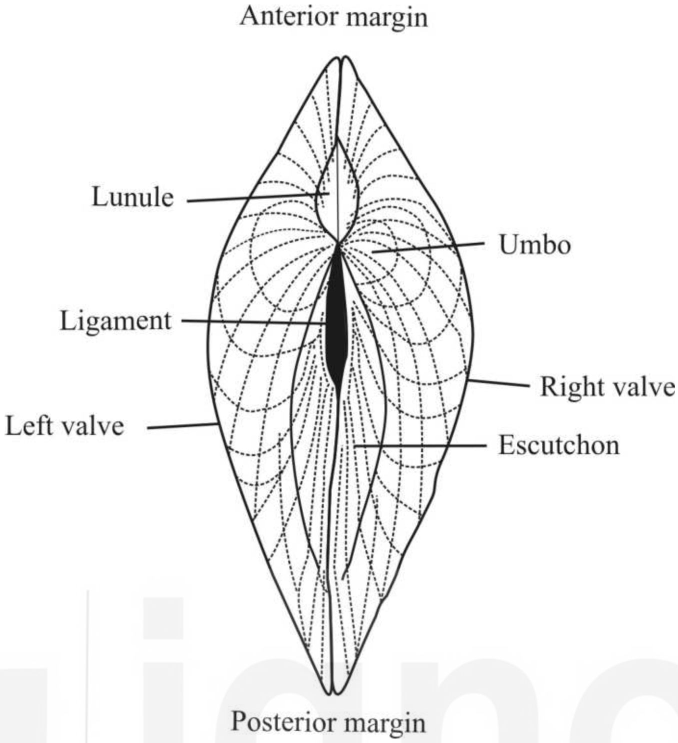


Fig. 14.2: Dorsal view of the shell showing external morphology of a bivalve.

If you see the internal surface of the valves, you can find the following features: muscle scars, pallial line, pallial sinus, teeth and sockets. Muscle scars are one of the important features of bivalve morphology. Indeed, these are the impressions or attachment sites left by the soft (fleshy) adductor muscles and commonly referred to as **adductor impressions** or **adductor scars**. Many bivalves have two adductor scars; one on the posterior margin, known as **posterior adductor scar** and the other on the anterior margin described as **anterior adductor scar** (Fig. 14.3). Based on the nature of adductor scar, bivalves are described as the following forms:

a) **Dimyarian**: two adductor scars (both anterior and posterior) are present.

b) **Isomayarian**: in this case, both scars are equal in size.

c) **Anisomyarian**: in these forms, the posterior scar is larger than the anterior adductor scar.

d) **Monomyarian**: includes those forms that are having one muscle scar only.

In dimyarian forms, two (anterior and posterior) adductor scars are connected to each other by a linear depression that runs more or less parallel to the ventral margin of the valve. This linear depression is known as **pallial line** (Fig. 14.3). In some cases, the pallial line exhibits an indentation or a fold near the posterior adductor scar, which is termed as **pallial sinus**.

It is interesting to note that muscles play a significant role in closing and opening of valves. When adductor muscles, located anteriorly and posteriorly, contract only then valves close and when these muscles relax, the ligament expands and valves open ventrally.

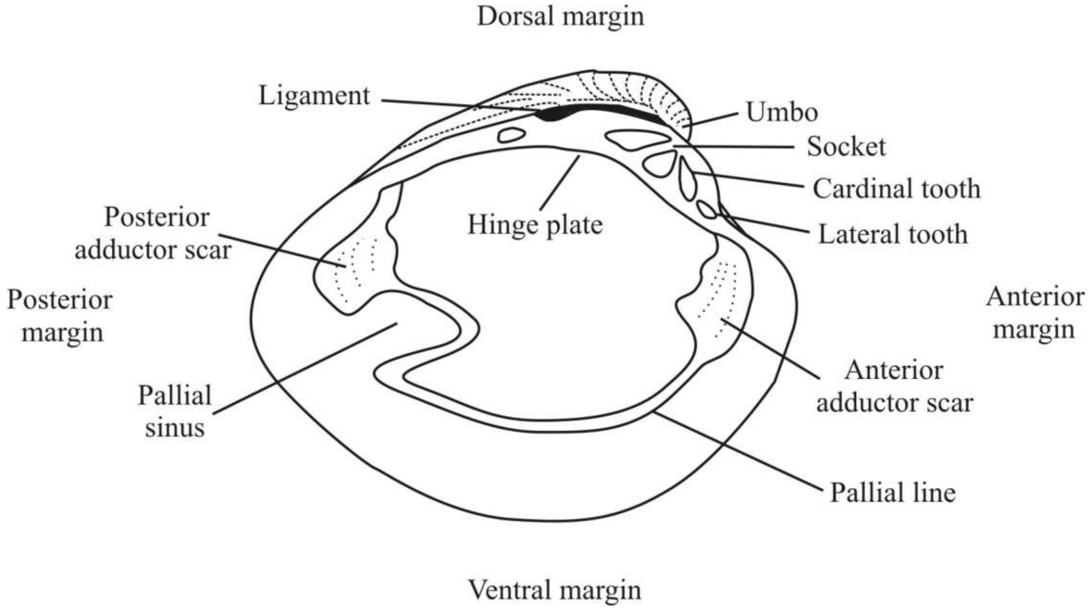


Fig. 14.3: Left valve of a bivalve showing internal (interior) morphology of a bivalve.

We have described earlier in this section that the two valves are joined dorsally by teeth and sockets. The portion of dorsal margin of valves, where teeth and sockets occur is known as **hinge line** or **cardinal margin**. The area lying between the hinge line and the umbo of each valve is called **hinge area**. In some cases, the hinge area is divided into a lunule and an escutcheon (Fig. 14.2). **Lunule** is a heart-shaped area that occurs in front of the beak and **escutcheon** is an elongated depression present posterior to the beak. The hinge line may be straight or curved and bears teeth and sockets. Both valves bear teeth and sockets alternatively and teeth of one valve fit into the corresponding socket of the opposite valve. This mechanism prevents the lateral motion of valves and keeps them tightly closed making it harder for a predator to open the shell by twisting the valves. Teeth and sockets are present in the beak region of the valves. The teeth present below the beak are termed as **cardinal teeth** and those that occur in front or towards the posterior side of the cardinal teeth are the **lateral teeth** (Fig. 14.3).

In bivalves, the term **dentition** is used to describe the arrangement of teeth, sockets and other closely related features. There are three types of dentitions present in bivalves: taxodont, schizodont and heterodont (Fig. 14.4).

a) **Taxodont**: it is a primitive type of dentition, where teeth are numerous, more or less equal in size and arranged in a subparallel pattern (Fig. 14.4a).

b) **Schizodont**: it includes two or three thick teeth with prominent grooves (Fig. 14.4b).

c) **Heterodont**: it comprises both cardinal and lateral teeth (Fig. 14.4c), which are not uniform and less in number.

The bivalve shells lacking dentitions are termed as **edentulous shells**.

Turning to the outside surface of the valves, you can see that in some cases it is smooth while in others it is ornamented with fine growth lines. The **growth lines** are concentric about the umbones and show the earlier positions of the edge of a valve. The outer surfaces may also be ornamented with other surface features such as radial ribs, concentric ridges and spines.

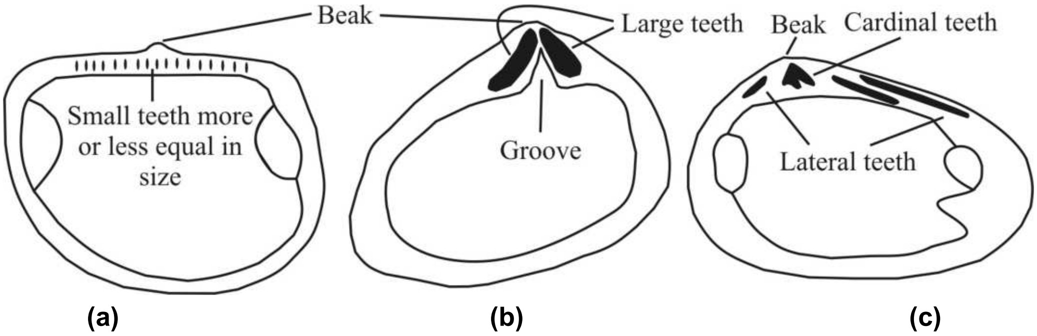


Fig. 14.4: Internal view of valves of bivalves showing different types of dentition: a) Taxodont; b) Schizodont; and c) Heterodont.

Key morphological features of bivalves: right valve, left valve, umbo, beak, adductor scars, pallial line, pallial sinus, teeth, sockets, hinge line, lunule, escutcheon, cardinal teeth, lateral teeth and growth lines.

14.3.4 Geological History

Like brachiopods, bivalves also have a very long geologic history. The earliest bivalves are known from the early Cambrian, but they became diverse during the Ordovician. Unfortunately, till date no bivalves have been reported from the middle and late Cambrian times. Several groups of bivalves arose during their Ordovician expansion. Such groups had taxodont and heterodont hinges and a wide range of feeding habits such as palp feeding, shallow burrowing, epifaunal and infaunal feedings. After the Ordovician expansion, bivalve diversity stabilised, but they did not emerge as a diverse group during the Palaeozoic (Fig. 14.5). The non-marine bivalves first arose in the Devonian and became abundant in the Carboniferous.

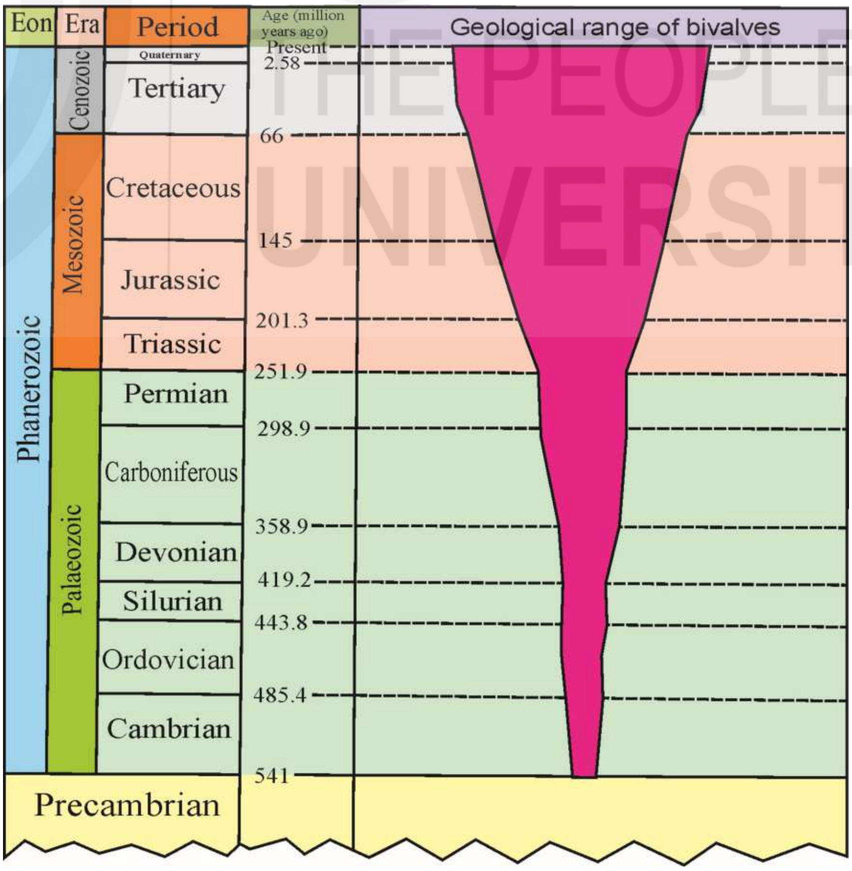


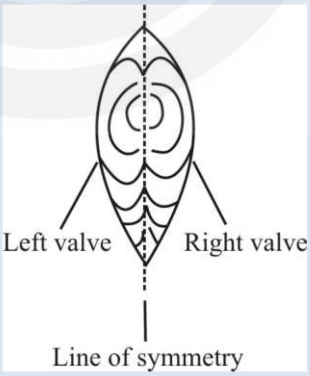
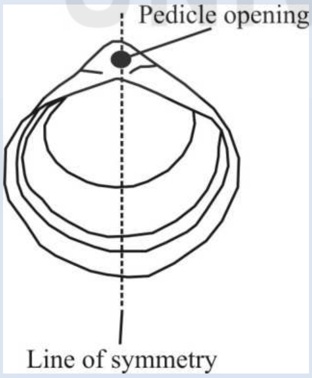
Fig.14.5: Stratigraphic distribution of bivalves. (Source: simplified after Jones, 2011)**. Width of column represents the abundance of bivalves in a particular period/era.**

Bivalves underwent a second great radiation during the early Mesozoic. Many new groups appeared during this radiation, several of which successfully adapted to the infaunal mode of life. Epifaunal bivalves also diversified in the Mesozoic. One group of bivalves, namely, rudists originated in late Jurassic and became extinct at the end of the Cretaceous. Except rudists, most other bivalves crossed the late Cretaceous mass extinction event and survive till date (Fig. 14.5).

14.3.5 Differences Between Bivalves and Brachiopods

As you know the shells of bivalves and brachiopods comprise two valves. For this reason, bivalves are often confused with brachiopods. For correct identification of these invertebrates, it is pertinent to know the differences between them. The major differences between them are given in Table 14.2.

Table 14.2: Main differences between bivalves and brachiopods.

Characters	Bivalves	Brachiopods (articulate)
Shell shape	Two valves are equal in size (i.e. equivalved).	Two valves are not equal in size (i.e., inequivalved).
Valves	Valves are left and right in position where each valve is a mirror image of the other	Valves are named as pedicle and brachial that are ventral and dorsal in position, respectively. Pedicle valve is bigger than the brachial valve.
Shell composition	Calcite or aragonite	Calcite
Shell symmetry	Bilaterally symmetrical with a plane of symmetry between valves (Fig. 14.6a).  Fig.14.6a: Shell of a bivalve showing plane of symmetry in dorsal view.	Bilaterally symmetrical with plane of symmetry along mid-line of each valve (Fig. 14.6b).  Fig. 14.6b: Pedicle valve of a brachiopod shell showing the plane of symmetry in internal view.
Dentition	Teeth and sockets usually present in each valve.	Teeth occur on pedicle valve and sockets on brachial valve. Inarticulate brachiopods lack teeth and sockets

Hinge mechanism	Ligament, teeth and socket interlock the valves	Teeth fit into sockets in the opposite valve. Ligament is absent.
Pedicle opening	Absent	Present

SAQ 1

a) What is the characteristic feature of a bivalve?

b) What is the primary function of ligament, teeth and sockets in bivalves? In which margin of the shell they occur.

c) Differentiate between beak and umbo?

d) Give the geological age range of Bivalvia.

14.4 GASTROPODS

Gastropods are the largest, most diverse and successful class of the phylum Mollusca. The class, Gastropoda (gas-tro-pod-a), comprises more than 50,000 known species, of which about 35,000 are living (extant) and around 15,000 extinct. It includes animals having a single valved (commonly known as univalved) shell like snails, limpets. However, in some cases, it also includes forms which have no hard shell like slugs. Gastropods first appeared in the early Cambrian and presently, they are distributed widely across the globe. Originally, they were marine animals, later they successfully occupied the land and fresh water environments. Nevertheless, the majority of gastropods remained marine and a very few groups adapted to freshwater and land conditions. During the course of their evolution, they have developed a wide range of locomotion modes such as creeping, floating and swimming and a remarkable range of feeding styles like grazing, predatory and parasitic.

14.4.1 What is Gastropoda?

As stated above, the gastropods (Class Gastropoda) represent one of the main groups of molluscs. A very common example of living gastropods, which you might have seen during the rainy season, is the garden snail. Besides garden snails, the other members of this class include slugs, limpets, periwinkles, coweries, nudibranchs and many others. It is interesting to note that all forms of gastropods do not possess hard shells. However, a majority of living gastropods (e.g., snails) and those preserved as fossils have single piece coiled hard shells. Some other forms like slugs have lost their shell and hence are not found as fossils. The average size of shells of gastropods is around 25 mm in length or diameter, but size of fully grown adults, ranges from 0.5 mm to around 60 cm (Moore and others, 1997).

Let us have a brief view of the soft parts of gastropods. The body of a gastropod is easily divisible into three parts: head, visceral mass, foot and mantle (Fig. 14.7). **Head** is a well-developed soft part of the gastropods and it bears a mouth, eyes and a pair of sensory tentacles. **Visceral mass** includes organs of the digestive tract. **Foot** is a muscular part of the body, which is used for slow creeping locomotion by the animal. In some cases, it can be modified in the swimming forms and becomes a useful tool in swimming. **Mantle** lies over the visceral mass and secretes the shell. Many gastropods are characterised by a process known as **torsion**, in which the visceral mass and mantle of the animal lie over its head (Fig. 14.7).

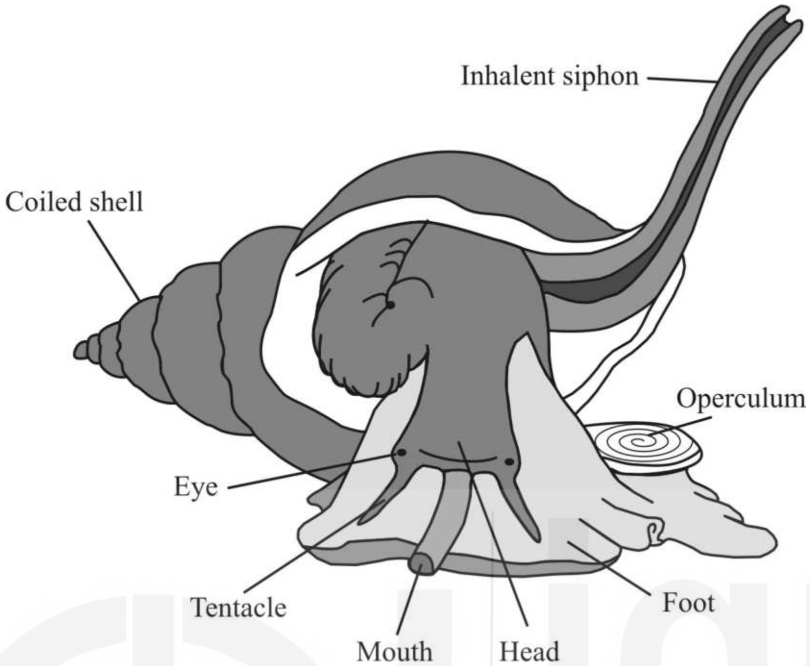


Fig. 14.7: Schematic diagram of a living gastropod showing the soft parts.
(Source: simplified after Clarkson, 1998; Jackson, 2010)

14.4.2 Systematic Palaeonotology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Mollusca
Class	Gastropoda
Subclass	Prosobranchiata
	Opisthobranchiata
	Pulmonata

Prosobranhiata: It includes primitive and marine forms of gastropods. They have a well-developed shell.

Examples – limpets, whelks and winkles.

Age range: Early Cambrian – Present.

Opisthobranchiata: It includes marine forms which have reduced or no shell. This group consists of sea slugs and sea hares.

Age range: Cambrian – Present.

Pulmonata: It consists of freshwater and terrestrial gastropods. This is the only group of molluscs that have made a successful transition from water to land. Many forms of this subclass have retained their shells except land slugs.

Examples – land snails and slugs

Age range: Mesozoic to Present.

Common genera of gastropods: *Planorbis*, *Natica*, *Turritella*, *Murex*, *Physa*, *Viviparus*, *Platyceras*, *Trochus*, *Nerita* and *Conus*.

14.4.3 Morphology

The body of most of the gastropods is made up of a shell, which is secreted by the mantle. The shell consists of a single valve and hence, it is commonly named as **univalve**. Chemically, it is made up of aragonite – a mineral of calcium carbonate ($CaCO_3$). In many gastropods, the shell is in the form of a spirally-coiled, screw-like long tube, which has an opening at one end and a tapering point at the other end. Each coil of the shell is known as **whorl** and the line between two neighbouring whorls is described as a **suture** (Fig. 14.8). The flattened part of each whorl, below the suture is termed as **shoulder**. The largest whorl of the shell is known as **body whorl** (Fig. 14.8). The body whorl ends in an opening, termed as the **aperture** that marks the region through which head and foot emerge (Fig. 14.8). The body whorl is the last fully developed whorl and marks the basal position of the shell. Combining all whorls, (except the body whorl) together constitutes the **spire** (Fig. 14.8). The pointed top end of the spire is known as the **apex** of the shell (Fig. 14.8). It is important to note that shells of many gastropods do not have tapering and pointed apex, but a flattened apex. The apex forms the posterior margin and aperture marks the anterior margin of the shell.

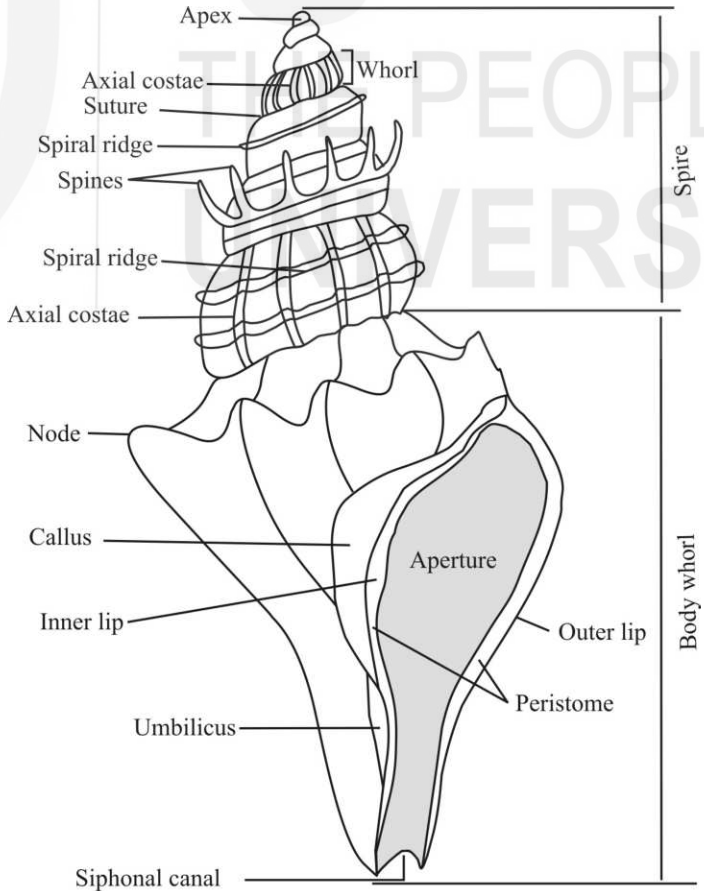


Fig. 14.8: Shell of a gastropod showing main morphological features. (Source: simplified after Shrock and Twenhofel, 1987)

In some gastropods, the tight coiling of inner parts of whorls fuses with the vertical axis of the coiling forming a central solid pillar like structure, which is termed as **columella** (Fig. 14.9). However, in some other forms, the inner parts of the whorls do not coalesce to form a solid columella and instead they are coiled around a hollow axial cone, which opens at the base of the shell and is termed as **umbilicus** (Fig. 14.8). Gastropod shells with columella are described as **imperforate** while those with umbilicus are known as **perforate**.

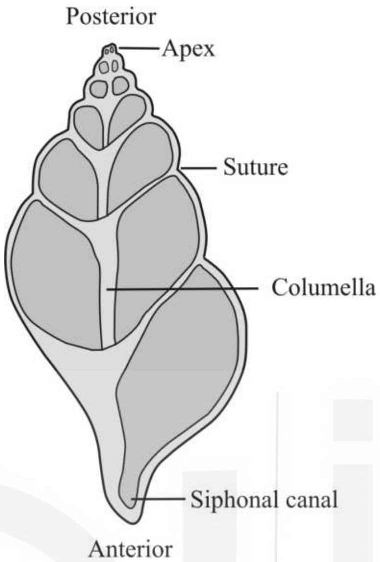


Fig. 14.9: Internal section of a gastropod shell showing the morphological features.

As you now know that most of the shells are coiled, and this coiling can be either dextral or sinistral. To know whether a shell is sinistral or dextral, it is important to orient the shell in such a way that its apex faces upward and aperture is visible to you. In this position, if the shell is coiled in anticlockwise direction and the aperture appears on the left hand side, then the shell is **sinistral** (Fig. 14.10a). In the same position, if the shell is coiled in clockwise direction and an aperture appears on the right hand side, then the shell is said to be **dextral** (Fig. 14.10b). In gastropods, dextrally coiled shells are more common, while sinistrally coiled shells are rare.

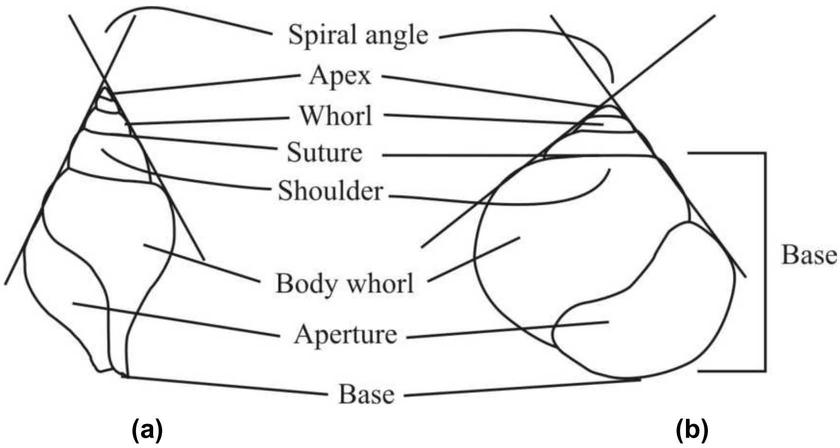


Fig. 14.10: Shells of gastropods showing morphological features: a) Sinistral; and b) Dextral shells.

The outline of an aperture may be simple, circular, oval, elliptical, crescentic or slit-like. The margin of the aperture is known as **peristome** (Fig. 14.8). The peristome is divided into two parts – inner lip and outer lip (Fig. 14.8). The margin of aperture lying towards the inner side of the last whorl close to the columella is the **inner lip** and the opposite margin is the **outer lip**. The outer lip may be sharp, thin or thickened and sometimes it may be curved inwards or outwards. When the outer lip is curved inwards, it is termed as **inflected**, when it is curved outwards, then it is described as **reflected**. Sometimes an outer lip shows a notch or **siphonal canal**, which is a semi-tubular extension of the aperture that holds the siphon (Figs. 14.8 and 14.9). **Siphon** is a soft inhalant tube that takes water into the mantle cavity when the animal is active. The peristome with siphonal notches is known as **siphonostomatous** and those without notches are described as **holostomatous**. Some gastropods have a shelly deposit termed as **callus** (Fig. 14.8), which is secreted by the mantle and commonly found near the inner lip of the aperture adjacent to the last whorl. This shelly callus sometimes closes the umbilicus of the shell. The aperture of many shells is sealed or closed by means of a calcareous disc or lid which is known as **operculum**. The operculum is attached to the upper part of the foot and it closes the aperture when the soft parts of the animal are withdrawn completely into the shell and hence, it provides protection to the animal (Fig. 14.7).

Turning towards the top of the shell, the shape of the apex of the shell is determined by the spiral angle. Spiral angle is measured by drawing two straight lines, in which each line is a tangent from the apex to the last two whorls on opposite sides and the angle subtended between them is the **spiral angle** (Fig. 14.10). In a high-spired shell, the spiral angle is an acute angle whereas it can be an obtuse angle in a low-spired shell. The first-formed or embryonic shell, which is found at the apex, is termed as **protoconch**. It is present in the larval shell and consists of several whorls which can be differentiated from later whorls by change of sculpture of the shell. The apex is the first-formed part and therefore, represents the oldest part of the shell.

You have learnt earlier that shells of gastropods exhibit spirally coiled structure, which is broadly of two types – conispiral and planispiral. **Conispiral** shells are coiled along an erect cone (Fig. 14.11a). The **planispiral** shells are those in which coiling is arranged symmetrically in a single plane (Fig. 14.11b). Most of the conispiral shells are dextral, but a few are sinistral. The coiled shells of gastropods display a number of forms. Some of the common forms are discoidal, conical, fusiform, evolute and convolute. In **discoidal** shells, all whorls are arranged in a single plane (Fig. 14.11c), while the **conical** shells have flat bases (Fig. 14.11d). **Fusiform** shells are spindle-shaped, being thickest in the middle and sharp-pointed at both ends (Fig. 14.11e). In normal situations, when all whorls are visible it is said to be **evolute** form (Fig. 14.11f). Some planispiral shells have a large last whorl which partially covers all the preceding whorls, such forms are called **convolute** (Fig. 14.11g).

The external or outer surface of shells may be smooth or ornamented by surface sculpture such as growth lines, ribs, spines, costae, knobs, and so on. **Growth lines** are the markings on the shell, which are parallel to apertural margin. **Coaste** are the thread-like thickenings of the shell, which run parallel to the spire (Fig. 14.8) and **ribs** are elevations on the surface of the shell that run parallel to the suture.

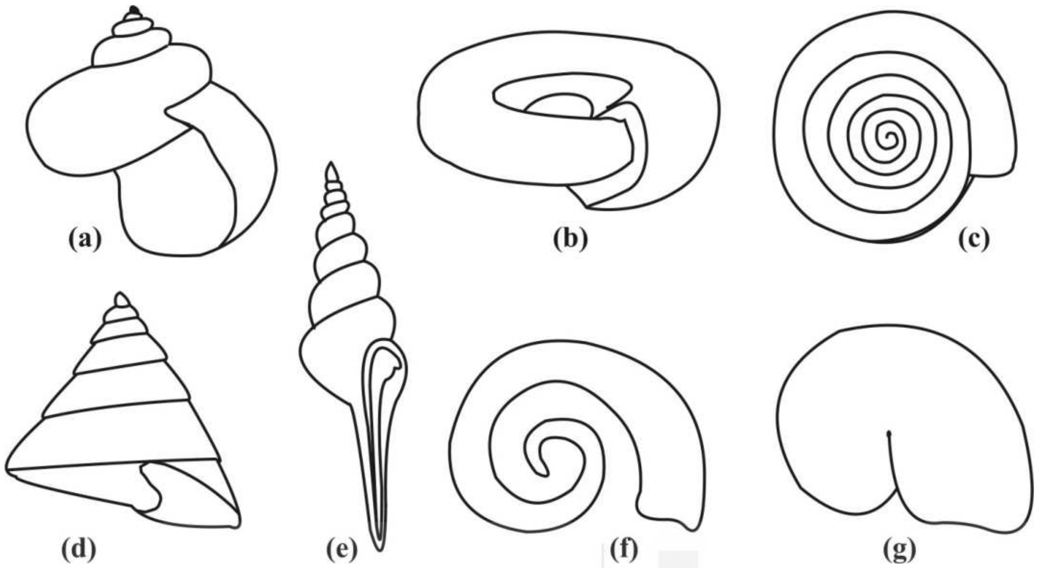


Fig. 14.11: Forms of gastropod shells: a) Conispiral; b) Planispiral; c) Discoidal; d) Conical; e) Fusiform; f) Evolute; and g) Convolute. (Source: simplified after Moore et al., 1997)

Key morphological features of the gastropods: univalve, whorl, spire, suture, body whorl, aperture, columella, umbilicus, peristome, siphonal canal, outer lip, inner lip, siphonostomatous, holostomatous, operculum, spiral angle and protoconch.

14.4.4 Geological History

The geological range of gastropods is from Cambrian to Recent (Fig. 14.12). The first gastropods appeared in the early Cambrian. These have simple, low and cup-shaped shells. They diversified during the Ordovician and colonised in the sea, freshwater and land during the Carboniferous. The oldest known pulmonate gastropods have been reported from the late Carboniferous. During the Palaeozoic, the holostomatous gastropods, belonging to the subclass Prosobranchiata were dominant. It is equally important to note that gastropods suffered from diversity loss during the late Palaeozoic, particularly in late Ordovician, late Devonian and late Permian.

During the Mesozoic, gastropods underwent the second phase of diversification (Fig. 14.12). As a result, siphonotomatous forms appeared in Triassic and became abundant in the late Jurassic. In the Mesozoic, land forms diversified dramatically during the late Jurassic and late Cretaceous, whereas marine forms diversified during the mid Cretaceous. Cenozoic witnessed the last phase of gastropod diversification. Presently, gastropods are widely distributed all over the globe. During the Meso-Cenozoic times, gastropods witnessed minor losses in their diversity (Jones, 2011). In the Cenozoic, the siphonostomatous forms were dominant and the pulmonate gastropods reached the peak of their diversity. At present, the gastropods are widely distributed in sea as well as on land and are adapted to a variety of habits and habitats.

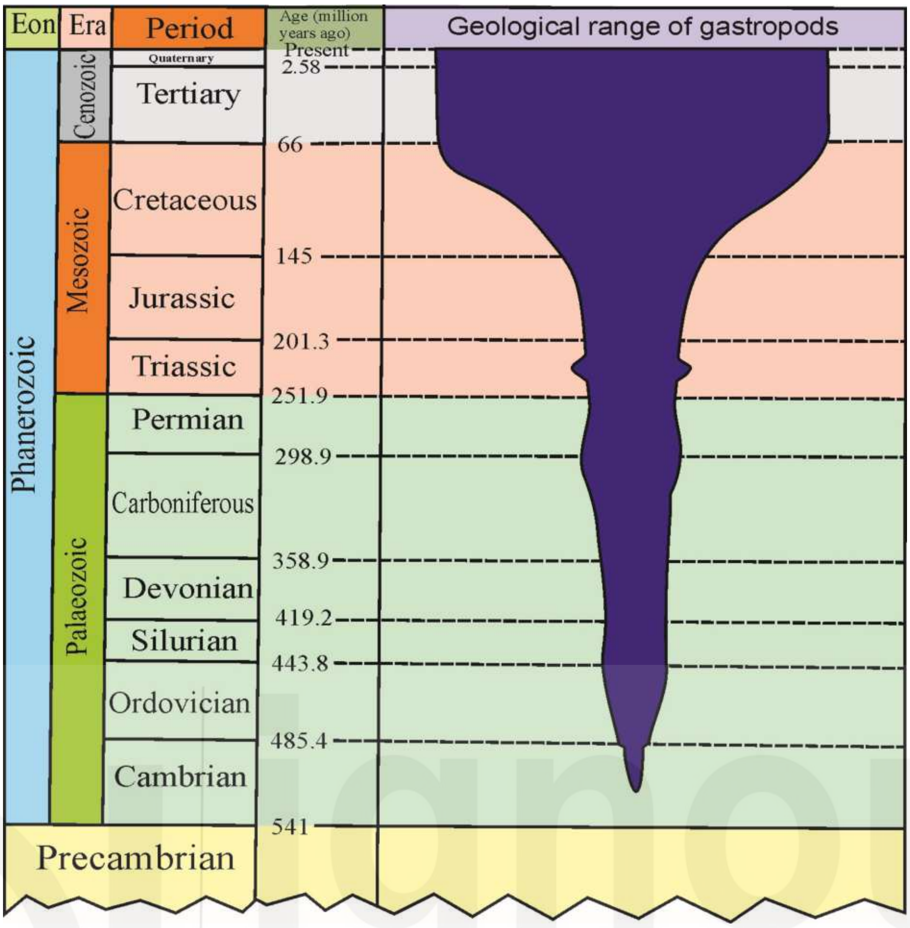


Fig. 10.12: Geological history of gastropods. Width of column represents the abundance of gastropods in a particular period/era.

SAQ 2

a) What are gastropods?

b) The shell of the gastropod is univalve. Yes/No

c) Define the terms: suture, body whorl, aperture and spire.

d) When do the pulmonate gastropods appear in the fossil record?

e) Name the three phases of gastropods diversitfication.

f) Match the following:

a. Operculum	i. Cambrian to present
b. Dextral shell	ii. Terrestrial
c. Peristome	iii. A calcareous disc or lid that is attached on the upper part of the foot
d. Pulmonate gastropods	iv. Outer margin of the aperture
e. Age of gastropods	v. Shell coiling clockwise and aperture appearing on the right hand side

14.5 ACTIVITY

In this unit, you have learnt about two groups of molluscs – bivalves and gastropods. Both these groups differ in a number of morphological features.

Illustrated below are two mollusc shells (Fig. 14.13). Determine the number of valves that each shell has and accordingly, identify the group.

Fig. 14.13: Shells of molluscs.

14.6 SUMMARY

In this unit, you have learnt the following:

- Molluscs possess a hard external shell (i.e., exoskeleton), which encloses their soft body parts such as head, muscular foot, mantle, gill and visceral mass.
- Bivaliva, Gastropoda and Cephalopoda are the major classes of the Phylum Mollusca that have a fossil record.
- Shell of bivalves is made up of two valves, namely, right valve and left valve.
- Right valve, left valve, beak, umbo, adductor scars, pallial line, pallial sinus, hinge line, lunule, escutcheon, teeth, sockets, growth lines and dentition are the major morphological features of bivalves.
- Shell of gastropods is made up of a single piece valve, known as univalve. All gastropods do not have hard shell.
- Whorls, suture, body whorl, spire, aperture, spiral angle, columella, umbilicus, peristome, siphonal canal, holostomatous, siphonostomatous, operculum, protoconch, growth lines, dextral, sinistral, planispiral coiling and conispiral coiling are the major morphological features of gastropods.
- Geological age of both bivalves and gastropods ranges from Cambrian to Recent. Bivalves diversified during the Ordovician period and Mesozoic era. Whereas, gastropods diversified during the Ordovician period and Mesozoic and Cenozoic eras.
- Bivalves are marine and fresh water animals while gastropods are marine, freshwater and land animals.

14.7 TERMINAL QUESTIONS

1. Describe and classify molluscs.
2. What are bivalves? Discuss the morphology of a bivalve.

3. How can you differentiate bivalves from brachiopods?
4. Describe the geological history of bivalves and gastropods.
5. Define the following morphological features of gastropods: columella, umbilicus, spiral angle, operculum, protoconch, holostomatous, siphonostomatous, dextral and sinistral.

14.8 REFERENCES

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- Shrock, R.R. and Twenhofel, W.H. (1987) Principles of Invertebrate Paleontology. CBS Publishers and Distributors Pvt. Ltd., New Delhi.

14.9 FURTHER/SUGGESTED READINGS

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- Shah, S.K. (2013) Elements of Palaeontology, Geological Society of India, Bangalore.

14.10 ANSWERS

Self Assessment Questions

1 a) The twin-valved shell is a characteristic feature of bivalves. The two valves are laterally compressed and are essentially mirror images of each other and united together dorsally by means of ligament, teeth and sockets.

b) Bivalves use ligament, teeth and sockets to open and close their valves. Ligament, teeth and sockets occur on the dorsal margin of the shell.

c)

Beak	Umbo
Beak is the nose-like pointed tip on each valve and represents the oldest part of the shell. It usually curves toward the anterior (i.e., front) end of the valve.	Umbo is the region of maximum curvature of each valve close to the beak and situated on the dorsal margin of the shell.

d) Cambrian to Present (Holocene/Recent).

2 a) Gastropods are the largest, diverse and most successful class of the phylum Mollusca. This class includes animals having a single valve (commonly known as univalve) shell like snails, limpets; however, in some other cases, it also includes forms which have no hard shell, for example, slugs.

b) Yes.

c) Suture is the spiral line that joins the surfaces of any two adjacent whorls of a gastropod shell. Body whorl is the last and largest whorl of the shell and it occurs near the basal margin of the shell. Aperture is an opening of the body whorl and spire is a combination of all whorls excluding the body whorl.

d) Carboniferous period.

e) The three phase of gastropods diversification are: 1) Ordovician diversification, 2) Mesozoic diversification and 3) Cenozoic diversification.

f) a. - iii., b. - v., c. - iv., d. - ii. and e. - i.

Terminal Questions

1. Refer to the 14.2.
2. Refer to the subsections 14.3.1 and 14.3.3.
3. Refer to the subsection 14.3.3
4. Refer to the subsections 14.3.4 and 14.4.4.
5. Refer to the subsection 14.4.3.

UNIT 15

MOLLUSCS – CEPHALOPOD

Structure

15.1 INTRODUCTION

In previous units (Unit 13 and 14), we have described four groups of invertebrates, namely, corals, brachiopods, bivalves and gastropods. These are either sessile or very slow moving animals. Among these, bivalves and gastropods belong to the phylum Mollusca and were described in Unit 14. Both these groups appeared in the Cambrian and some of them have persisted to the present.

In this unit, we shall deal with another intriguing and diverse group of molluscs – the **Cephalopoda**. Cephalopods are marine animals. They are more active, quick movers, intelligent carnivorous predators with varied shell morphology and highly developed nervous and visual systems. In these respects, they differ greatly from other molluscs. The Class Cephalopoda consists of three subclasses, among which Nautiloidea and Ammonoidea are commonly found asfossils. Coleoidea, the third subclasses, comprises primarily soft bodied animals. We will, very briefly, describe the basic organisation and classification of cephalopods and concentrate on the shell morphology and geological history of nautiloids and ammonoids in this unit. We will also discuss the functional adaptations in ammonoids in the latter part of the unit.

Expected Learning Outcomes

After reading this unit, you should be able to:

- ❖ define and classify cephalopod molluscs;
- ❖ describe the shell morphology of nautiloids and ammonoids;
- ❖ discuss the geological history of nautiloids and ammonoids;
- ❖ differentiate nautiloids from ammonoids; and
- ❖ explain the functional adaptations in ammonoids.

15.2 CEPHALOPODS

Cephalopods are a diverse, highly evolved and morphologically complex class of molluscs. They are exclusively marine animals that occupy the same ecological niche as fishes. This class includes extinct ammonoids and belemnites, and modern forms such as cuttlefish, squids, octopuses and nautilus. Like fishes, cephalopods are equipped with highly developed eyes and sensory organs. In addition, they are adapted to fast swimming and have developed more efficient mechanisms to locate their prey, detect predators and to escape from them. As a consequence, they live largely as marine predators. They have also been among the dominant group of predators in the sea at various times in geological history. Cephalopods comprise the largest invertebrates known and include some forms, which attained a length of about 16 m (Moore and others, 1997). It is important to note that many present day cephalopods like squids, cuttlefish and octopuses do not have an external shell (exo-skeleton). However, some of them have an internal shell (endo-skeleton). Nautilus is the only living cephalopod that has an external shell. The genus *Nautilus* is the only survivor among the nautiloids, which is a very ancient group of cephalopods.

You have read above that *Nautilus* is the single living genus of cephalopods that retains an external shell. This coiled calcareous ($CaCO_3$) shell provides an excellent opportunity to the palaeontologists to understand the soft anatomy of shelled cephalopods. Therefore, we will use the genus *Nautilus* to describe the soft anatomy of cephalopods. The soft parts of *Nautilus* show bilateral symmetry and consist of visceral mass, mantle cavity, well-defined head and foot (Fig. 15.1). The **visceral mass** is located in the rear body (living) chamber. The **head** and **foot** are fused closely together; head bears mouth and a pair of eyes. Foot is modified into many tentacles, which are used mainly for locomotion and catching the prey. Above the head, there is a tough fleshy fold termed as **hood**. When an animal withdraws into the living chamber of the shell, the hood acts as an operculum and closes the aperture of the living chamber. Mouth of *Nautilus* is equipped with radula and two parrot's beak shaped jaws that open inside the circle of tentacles. Below the tentacles is **hyponome** or **funnel** (Fig. 15.1). Hyponome is a muscular organ modified from the foot and it can be turned in any direction. It provides an opening to the mantle cavity that contains gills and anus. When water enters the mantle cavity and passes over the gills and if the water is forcibly ejected back from the mantle cavity, the hyponome acts as a jet to propel the animal backward or forward depending upon the direction of the hyponome. In this way, the animal moves backward and forward. The soft parts of *Nautilus* are fully enclosed by the mantle and the mantle is enclosed by the external shell.

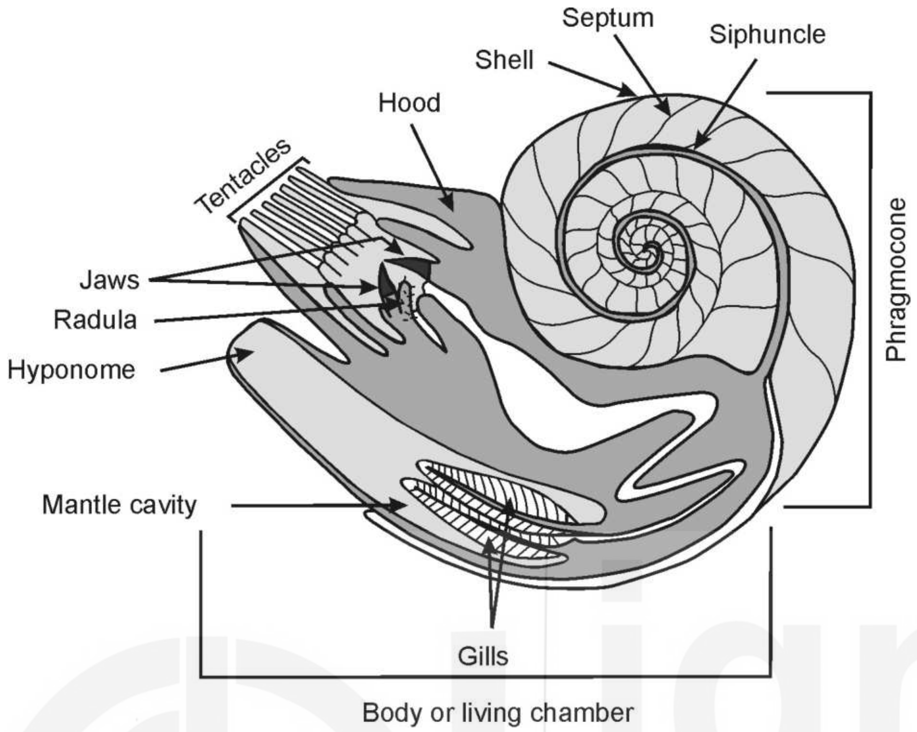

Fig. 15.1: Schematic diagram of living *Nautilus* showing main morphological features. (Source: simplified from Clarkson, 2007; Milsom and Rigby, 2010)

15.2.1 Classification of Cephalopods

The classification of cephalopods is still a debated issue. Biologists classified cephalopods on the basis of number of gills, but this classification is not accepted by the palaeontologists, because a majority of cephalopods are extinct and no one knows how many gills those extinct forms had. Palaeontologists classify cephalopods into three subclasses on the basis of their shell morphology (Table 15.1).

Table 15.1: Classification of cephalopods. (Source: simplified from Clarkson, 2007; Benton and Harper, 2009).

Phylum	Mollusca
Class	Cephalopoda
Subclass	**Nautiloidea** Characteristic features: Straight, curved or coiled external shell with simple suture; simple surface sculpture. Four gills are present. Example – *Nautilus* Age range – Late Cambrian to Present
Subclass	**Ammonoidea** Characteristic features: Coiled external shell with complex surface sutures; complex surface sculpture. Gill count is

	unknown. It is an extinct subclass of cephalopods Example - *Ammonites* Age range – Early Devonian to Late Cretaceous
Subclass	**Coleoidea** Characteristic features: Straight or coiled internal shell and two gills are present. Examples – squid, cuttlefish, octopus and extinct *Belemnites.* Age range – Carboniferous to Present.

Shells of cephalopods are borne either internally or externally. Nautiloidea and Ammonoidea have external shells while some members of the subclass Coleoidea have internal shells. However, the main elements of cephalopod shell architecture are the same in both external and internal shells (Nield and Tucker, 1985).

Generally, shells of cephalopods are chambered and each chamber is separated by a wall known as **septum** (Fig. 15.1). Chambers are produced as the animal grows and expands. As the animal grows, it also seals off the older chambers in the shell which are filled with gas, making the shell buoyant and helping the animal to swim. The animal always sits in the last chamber known as **body** or **living chamber** (Fig. 15.1). The animal living in the body chamber maintains contact with the others chambers by siphuncle (Fig. 15.1). The term **phragmocone** is used to describe other chambers except the body chamber. **Siphuncle** is a tube that passes through the centre of each septum (plural septa) and connects the chambers. Siphuncle helps the animal to maintain the gas pressure in each chamber and control its buoyancy. The nature of the septa and siphuncle is very important for identifying whether the shell belongs to nautiloids or ammonoids. We will now discuss the nautiloids and ammonoids separately in the following sections.

15.3 NAUTILOIDS

Nautiloids are a large and diverse group of cephalopods (Fig. 15.2). They belong to the subclass Nautiloidea. They are marine, first appeared in the late Cambrian and are considered as the probable ancestral stock from which all other cephalopods have evolved. Around 2500 fossil species of nautiloids are known, but, today they are represented by a single living genus – *Nautilus*. The study *Nautilus* helps the palaeontologists to understand the relationship of the hard parts to the behaviour of the nautiloids. The studies on *Nautilus* show that it pursues a nocturnal mode of life both as a predator and scavenger. Nautiloids are characterised by the presence of an external shell. Since *Nautilus* has four gills by analogy, it is assumed that extinct nautiloids probably also had four gills. Nautiloids range in size from a few centimeters to several meters in length. The largest nautiloid fossil recorded, so far, is 4 m in length.

Fig. 15.2: Shell of a nautiloid. (Source: Prof. R. Nagendra, Anna University)

15.3.1 Systematic Palaeonotology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Mollusca
Class	Cepalopoda
Subclass	Nautiloidea

Common genera of nautiloids: *Nautilus, Centroceras, Oncoceras, Endoceras, Piloceras, Actinoceras* and *Discosorus.*

15.3.2 Morphology

Nautiloids have a chambered external shell, which is secreted by the mantle and made up of aragonite, which is a mineral of calcium carbonate. The shell is tabular in form and may be straight, curved or spirally coiled. It is a hollow cone with two main parts – body or living chamber and phragmocone (Fig. 15.3a). As stated earlier, shells of nautiloids are generally chambered, in which each chamber is formed when an animal living in the body chamber grows and widens the shell, and moves forward towards the ever-growing aperture. Each time this process leaves a space behind the body, which is repeatedly walled off by a **septum** thus forming a series of chambers (Nield and Tucker, 1985). Shell consists of a tube, which is open at the larger end and closed at the smaller end. The opening present on the larger end is termed as **aperture** and the tip of the smaller end is the **apex** of the shell (Fig.15.3a). The aperture has a small notch cut on its ventral margin, which provides greater flexibility of movement to hyponome, which is known as **hyponomic sinus** (Fig. 15.3a).

Normally, the shell chambers increase in size from the apex (for embryonic shells, it is termed as protoconch) towards the aperture. As a result, the inner whorls are partly or fully covered by the outer whorls (Fig. 15.3a). **Whorl** is a single complete turn of the shell coiling and shells may have several whorls. The space enclosed on both sides by the last whorl is described as **umbilicus** (Fig. 15.3a). In spirally coiled forms, the whorls may be separate and loosely or tightly touching each other. The gap between two successive whorls is termed as **whorl gap**.

Orientation of the shell: The margin of the shell towards aperture is anterior and towards the apex is posterior. The side of the shell near the mouth and hyponome is ventral and opposite side is dorsal. Dorsum is the dorsal side and venter is the ventral side of the shell.

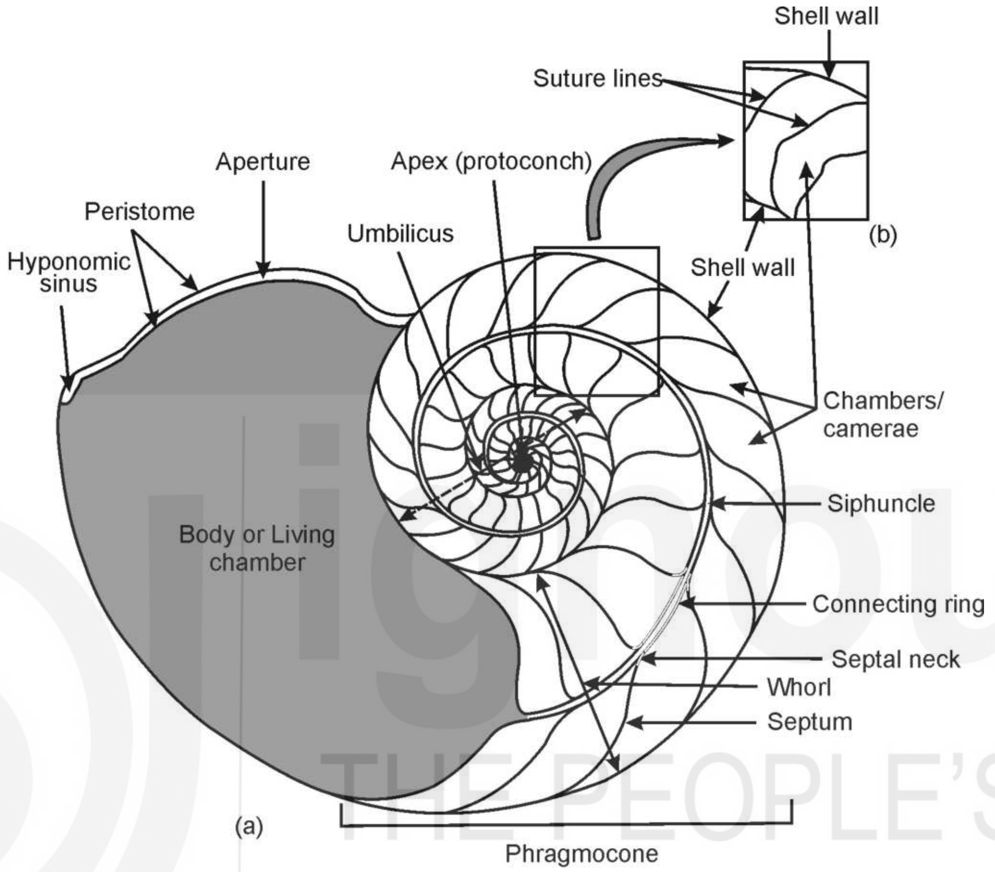

Fig. 15.3: Shell of a nautiloid: a) showing internal morphology; and b) enlarged part showing the suture lines.

Turning to the interior or internal surface of the shell, you can see that the shell is divided into a number of **chambers** or **camerae** by transverse partitions known as **septa** (Fig. 15.3a). The chambered portion (except last chamber) of the shell is known as **phragmocone** (Fig. 15.3a). In fact, phragmocone is the only part of the shell which is commonly preserved as fossil. The last chamber, which is the largest and occupied by the animal, is termed as **living** or **body chamber**. All chambers except the body chamber are filled with gas and they are also known as **gas chambers**. A thin calcareous tube which runs through the centre of each septum and connects all chambers is known as **siphuncle** (Fig. 15.3a). The siphuncle allows the exchange of gas between the living animal which resides in the body chamber and previously formed chambers. Siphuncle is composed of septal necks and connecting rings (Fig. 15.3a). **Septal necks** are short funnel-like structures, which are developed around the opening in each septum. **Connecting rings** are the shelly tabular structures, which connect the septal necks. The line where each septum joins the external surface of the shell is termed as **suture line** (Fig. 15.3b). In nautiloids, the suture lines are either straight or slightly curved (Fig.15.8a). The simple suture of nautiloids is also known as **nautiloid suture**. You can see suture lines only after the removal of the shell wall or in well preserved casts of nautiloids. It is important to note that siphuncle, suture line and septal necks are important morphological features, which distinguish nautiloids from ammonoids. In nautiloids, siphuncle passes through the centre of each septum, suture line is usually simple or sometimes, it may be straight or undulating and septal neck lies on the convex side of each septum and is projected towards the apex (protoconch) of the shell. Nautiloids generally have additional skeletal material on the bottom of chambers called **cameral deposits**. These deposits help the animal to keep itself perfectly oriented in marine waters. In the absence of cameral deposits, it would be difficult for the animal to stay in the right position (Jackson, 2010).

Key morphological features of nautiloids: body chamber, phragmocone, septa, aperture, siphuncle, suture, septal necks, connecting rings, whorls and cameral deposits.

The shells of nautiloids display a variety of forms. A straight conical shell is known as **orthoceracone** (Fig. 15.4a). Slightly curved shells are described as **cyrtoceracones** (Fig. 15.4b), loosely coiled shells are termed as **gyroceracones** (Fig. 15.4c) and shells having all whorls in contact are **traphyceracones** (Fig. 15.4d). Eccentric coiled shells are known as **trochoceracones** (Fig. 15.4e) and when the body whorl covers all other whorls, the shell is known as **involute nautilicone** (Fig. 15.4f) and in **evolute nautilicone** shells, the earlier formed or older whorls are all visible (Fig. 15.4g). A curved or straight shell is said to be **exogastric** if the ventral side is convex (curve outside) and dorsum is on the inside (Fig. 15.4h). A shell is said to be **endogastric** if the dorsal side is convex (curve outside) and venter is on the inside (Fig. 15.4i).

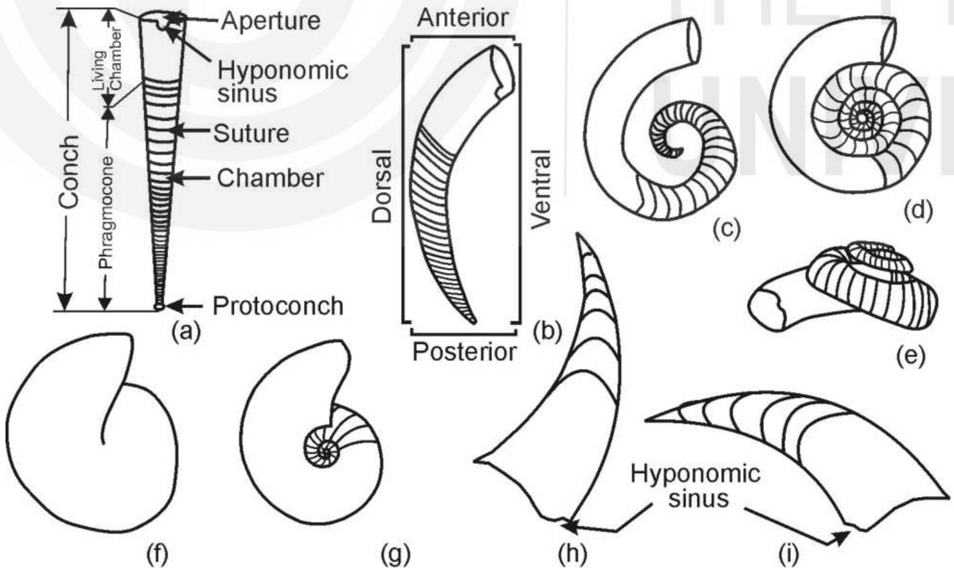

Fig. 15.4: Shells of a nautiloids showing various shell forms: a) Orthoceracone with main shell features; b) Cytoceracone showing the ventral, dorsal, anterior and posterior margins; c) Gyroceracone; d) Traphyceracone; e) Trochoceracone; f) Involute nautilicone; g) Evolute nautilicone; h) Exogastric; and i) Endogastric shell forms. Note that figures 15.4h and 15.4i are similar to figures 15.9g and 15.9h; the position of siphuncle helps us to determine whether the shell belongs to nautiloid or ammonoid. (Redrawn after Shrock and Twenhofel, 1987)

Turning to the outside surface of the nautiloid shells, you can see that some shells may be smooth or unornamented (e.g., *Nautilus*) while others, have only a feeble ornamentation in the form of growth lines, which is the most common surface feature.

15.3.3 Geological History

It is worth noting that the subclass Nautiloidea comprises about 300 genera and 2500 species, all of which are extinct and the subclass is now represented by a single genus *Nautilus* (Shrock and Twenhofel, 1987). There are a very few species, which represent the genus *Nautilus*. The nautiloids include the oldest known cephalopods. They first appeared in the fossil record during the late Cambrian having a simple curved shell. They rapidly diversified during the Ordovician and most of the groups arose during this time. Ordovician nautiloids are marked by the presence of straight or curved shells, which are much larger than the Cambrian nautiloids. It should be noted that the order Nautilida, in which the living genus *Nautilus* falls, appeared in late Silurian or early Devonian times. Nautiloids remained abundant and were a widespread component of the marine biota during the early Palaeozoic (Fig. 15.5a). They were also the primary predators of the Palaeozoic seas and their shells have a wide variety of forms ranging from straight to curved as well as spirally coiled.

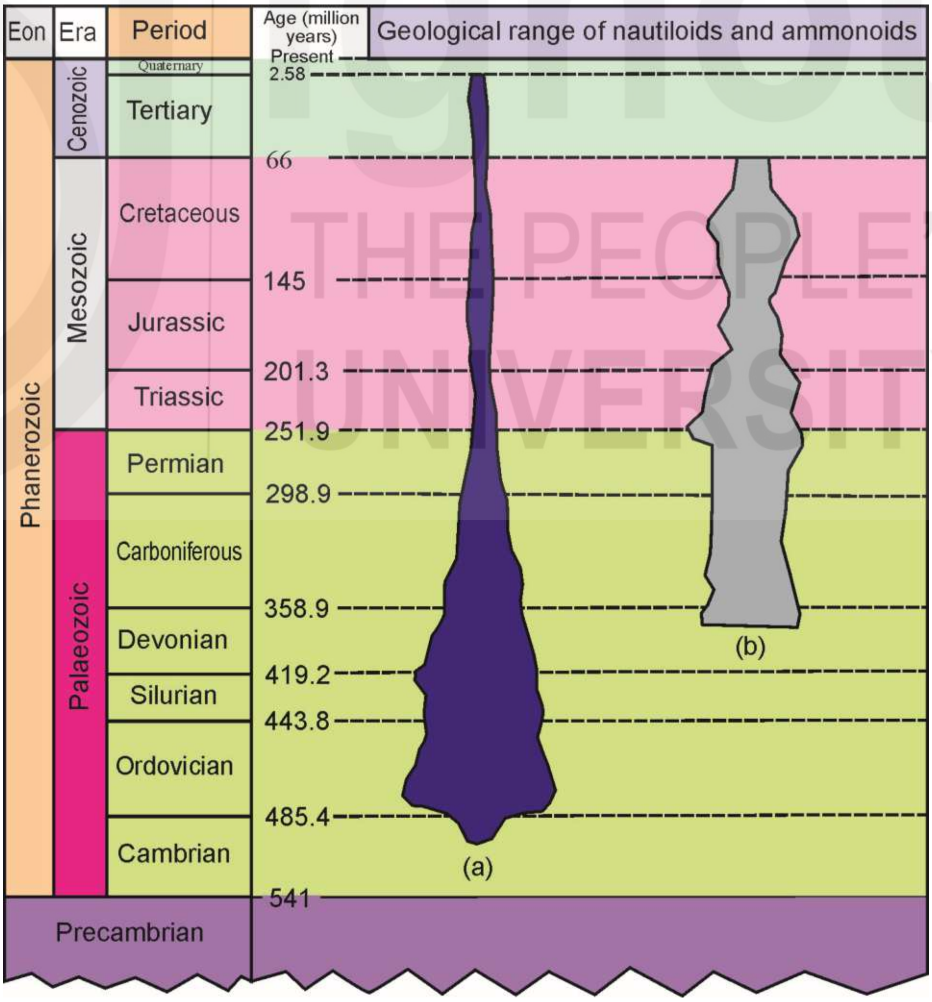

Fig. 15.5: Stratigraphic distribution of cephalopods: a) Nautiloids; and b) Ammonoids. (Source: modified after, Milson and Rigby, 2010)**. Width of column represents the abundance of nautiloids and ammoniods in a particular period/era.**

Nautiloids began to decline during the late Palaeozoic (Fig. 15.5a). Studies suggest that nautiloids are the probable stocks from which other cephalopods such as ammonoids and coleoids originated during the late Palaeozoic. The competition of nautiloids with their close relatives, like ammonoids and coleoids, is considered as one of the reasons behind their late Palaeozoic decline. Most of the Palaeozoic nautiloids became extinct by the end of Permian and only the order Nautilida having coiled shell, survived from Mesozoic to the present (Fig. 15.5a). Therefore, *Nautilus* is well known as a "living fossil" that typically belongs to a group with an old rich fossil history and which has not changed much morphologically over the long geological time.

SAQ 1

a) What is phragmocone?

b) Shells of nautiloids are composed of ……………. . (Aragonite/Calcite)

c) How can you differentiate between exogastric and endogastric shells?

d) Write the diagnostic morphological features of nautiloids.

15.4 AMMONOIDS

Ammonoids are an extinct group of marine cephalopod molluscs. They belong to the subclass Ammonidea and class Cephalopoda of the Phylum Mollusca. Ammonoids constitute the largest and one of the most important subclasses of Cephalopods. They lived in all the oceans of the world from early Devonian to late Cretaceous. It is generally accepted that ammonoids evolved from the genus *Bactrites*, which has a more or less straight shell and belongs to suborder Bactritina of the subclass Ammonoidea (Clarkson, 2007). As mentioned above Ammonoidea is an extinct class of cephalopods and very little is known about its soft parts morphology. It is considered that the soft parts of ammonoids must have been similar to those of nautiloids. However, it is also found that the biological affinities of ammonoids are more similar to those of coleoids than to *Nautilus*. Coleoidea is one of the subclasses of cephalopods, which include forms such as squids, cuttlefish, octopuses and extinct *Belemnites*, that have either no shell or an internal shell. There are some key features, such as the presence of seven teeth on radula, upper jaws that are very similar to the jaws of living octopuses and presence of ink sacs in fossil ammonoids, which place ammonoids closer to the coleoids than nautiloids (Clarkson, 2007).

Do you know?

In Indian mythology, the local people of Himalayan regions see ammonoids as the symbols of Lord Vishnu, the supreme God of the Hindus and are referred them to as Saligrams. Many living cephalopods have an ink sac, which is a muscular bag that contains dark ink. When in danger, the animal releases ink into the water, forming a dark cloud. This enables the animals to confuse the predators enabling it to escape. All cephalopods, except *Nautilus* and octopuses, are able to release ink. Fossil ammonoid shells also show preserved sites where ink sacs occurred.

Ammonoids had an external chambered shell (Fig. 15.6), which usually shows planispiral coiling, but there are some forms which exhibit either helically-spiraled coiling or no coiling. It is worth noting that most ammonoids had coiled shells of a similar form and look very similar to the living *Nautilus*. The spirally coiled nature of the shell is responsible for the derivation of the subclass's name Ammonoidea.

Fig. 15.6: Shell of an ammonite.

The diameter of ammonoids, ranges from less than 3 mm to more than 3 m. Ammonoids with 2 m diameter are known from the Upper Cretaceous sediments of the Cauvery Basin, Tamil Nadu, south India. It has been observed that sexual dimorphism was common in ammonoids. Based on the sexual dimorphism, ammonoids shells are classified into two types – macroconchs and microconchs. **Macroconchs** are larger shells and usually belong to females, whereas **microconchs** are small shells, which belong to males. It should be noted that number, size and morphology of whorls is an important criteria to differentiate macroconchs and microconchs.

15.4.1 Systematic Palaeonotology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Mollusca
Class	Cepalopoda
Subclass	Ammonoidea

Common genera of ammonoids: *Bactrites, Goniatites,* Discoclymenia, *Calliphylloceras, Katroliceras, Ataxioceras* and *Ptychophylloceras*.

15.4.2 Morphology

It is very important to note that the morphology of ammonoids is very similar to that of nautiloids. However, ammonoids can easily be differentiated from nautiloids on the basis of location of siphuncle, suture patterns and nature of septal necks. The ammonoid shells are either tightly coiled on a single plane (i.e., planisprial) or open helical and irregular coiled as well as straight. The planisprial coiled shells are known as **homomorph ammonoids** (Fig. 15.7) whereas straight, helical or irregular coiled shells are known as **heteromorph ammonoids** (Fig. 15.9a-c).

All ammoniods had an external chambered shell, which is divisible into three parts, namely, a) protoconch, b) phragmocone and c) body or living chamber. The earliest or the first formed chamber, located usually in the centre of the shell, is termed **protoconch** (Fig. 15.7). The term protoconch is used for embryonic forms and shell is applied for adult forms. The chambered portion of the shell is known as **phragmocone** (Fig. 15.7). The last chamber, which is the largest and occupied by the animal, is described as **living** or **body chamber** (Fig. 15.7). The opening present on the body chamber is termed **aperture**. The margin of the aperture is described as the **peristome** (Fig. 15.7). A single complete turn of the shell coiling is called a **whorl** and ammonoid shells may have several whorls. The hollow cone shaped space enclosed on both sides by the last whorl is described as **umbilicus** (Fig. 15.7). In spirally coiled forms, the whorls may be separate and loosely or tightly touching each other. The gap between the two successive whorls is termed **whorl gap**.

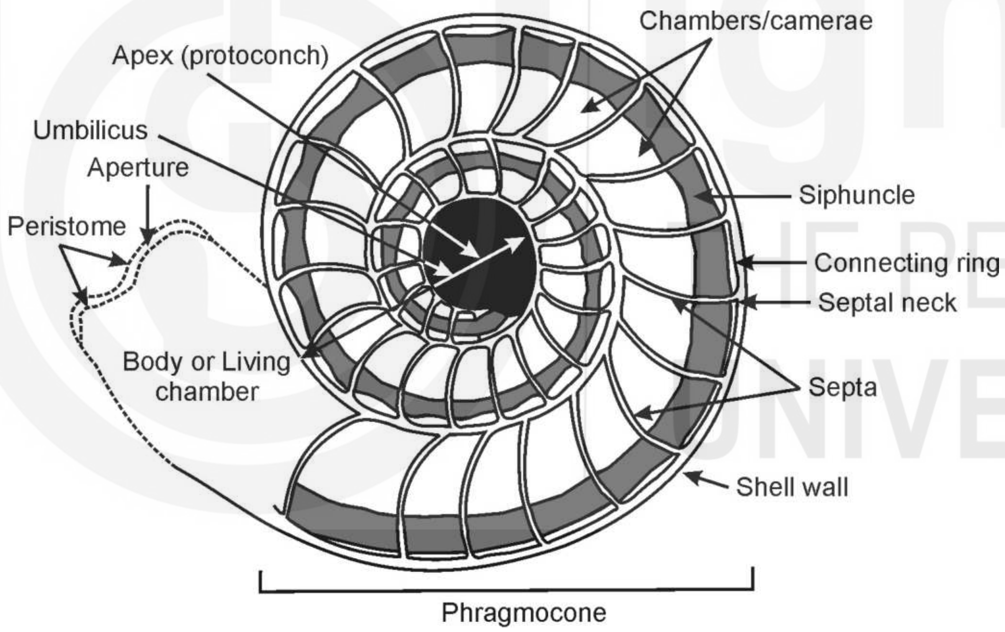

Fig. 15.7: Shell of an ammonoid showing morphological features (Source: simplified after Wood, 2004.

Turning to the interior or internal surface of the shell, you may find that phragmocone comprises a number of **chambers** or **camerae** (Fig. 15.7). Each chamber is marked by the successive occupation by the animal and separated by a septum (plural septa) (Fig. 15.7). You may recall that **septa** are the transverse partitions present between the chambers. Like *Nautilus,* when ammonoids grew, they also moved forward in the body chamber and secreted a septum at the back of the mantle and created a series of chambers. The chambers of ammonoids were formed in such a way that the gas filled in them creates a near neutral buoyancy similar to the chambers of nautoloids. A thin calcareous tube running through the ventral margin of septum and connects all chambers is known as **siphuncle** (Fig. 15.7). The siphuncle allowed the exchange of gas between the living animal, which sat in the body chamber and the previously formed chambers. In addition, animals may have used the siphuncle to pump water in or out of the chambers in order to alter the buoyancy of the shell. Siphuncle is composed of two parts, namely, septal necks and connecting rings (Fig. 15.7). **Septal necks** are short funnel-like structures developed around the opening in each septum whereas **connecting rings** are the shelly tabular structures, which connect the septal necks. In ammonoids, the septal necks are directed towards the aperture of the shells and connecting rings are placed towards the outer margin of the shell.

The line where a septum joins the external surface of the shell is termed as **suture line** (Fig. 15.8). The suture pattern is very complex in ammonoids. As a result, it forms one of the most important characteristic features on the basis of which one can differentiate ammonoids from nautiloids. If you remember what type of suture nautiloids have from the previous section, then it will be easy for you to understand the suture pattern of ammonoids. The nautiloids have a very simple suture without having any ridges (saddles) and grooves (lobes), whereas ammonoids have a complex suture pattern, in which suture line is composed of ridges and grooves (Fig. 15.8). The ridges pointing upwards (i.e., towards the aperture) are known as **saddles** and grooves pointing downwards (i.e., opposite direction of the saddles) are described as **lobes**. Three important types of sutures are recognised in the ammonoids, which are: a) Goniatitic, b) Ceratitic and c) ammonitic sutures. Now, we will discuss each one by one.

a) **Goniatitic Suture line**: It is characterised by rounded saddles and angular or sharp lobes (Fig. 15.8b). It is commonly found in ammonoids of the late Devonian to Permian age.

b) **Ceratitic Suture Line**: This suture line is characterised by smooth rounded saddles and finely divided to undivided lobes (Fig. 15.8c). It is found in ammonoids of Triassic age.

c) **Ammonitic Suture Line**: It is marked by complex and finely subdivided saddles and lobes (Fig. 15.8d). Ammonoids of Jurassic and Cretaceous age show ammonitic sutures.

Some shells of ammonoids have either a single horny plate or two equal sized calcareous plates, which are commonly found near the opening (i.e., aperture) of the shells. If the shell has a single horny plate, it is known as **anaptychus** and if it has two calcareous plates, it is termed as **aptychus**. Initially, it was argued that animal used such plate/s to shut the aperture as the gastropods use the operculum. Later, it was suggested that it is a part of a jaw apparatus. Majority of ammonoid shells show bilateral symmetry, which is a characteristic feature of those ammonoids that live with the median plane of the body in a vertical position. It is generally, believed that bilateral symmetry and vertical position were more likely to be retained by the swimming molluscs (Woods, 2004).

Key morphological features of ammonoids: body chamber, phragmocone, septa, aperture, ventral siphuncle, goniatitic suture, ceratitic suture, ammonitic suture, septal necks, connecting rings, whorls, anaptychus and aptychus.

The ammonoid shells display a variety of forms. Some common shell forms are described below:

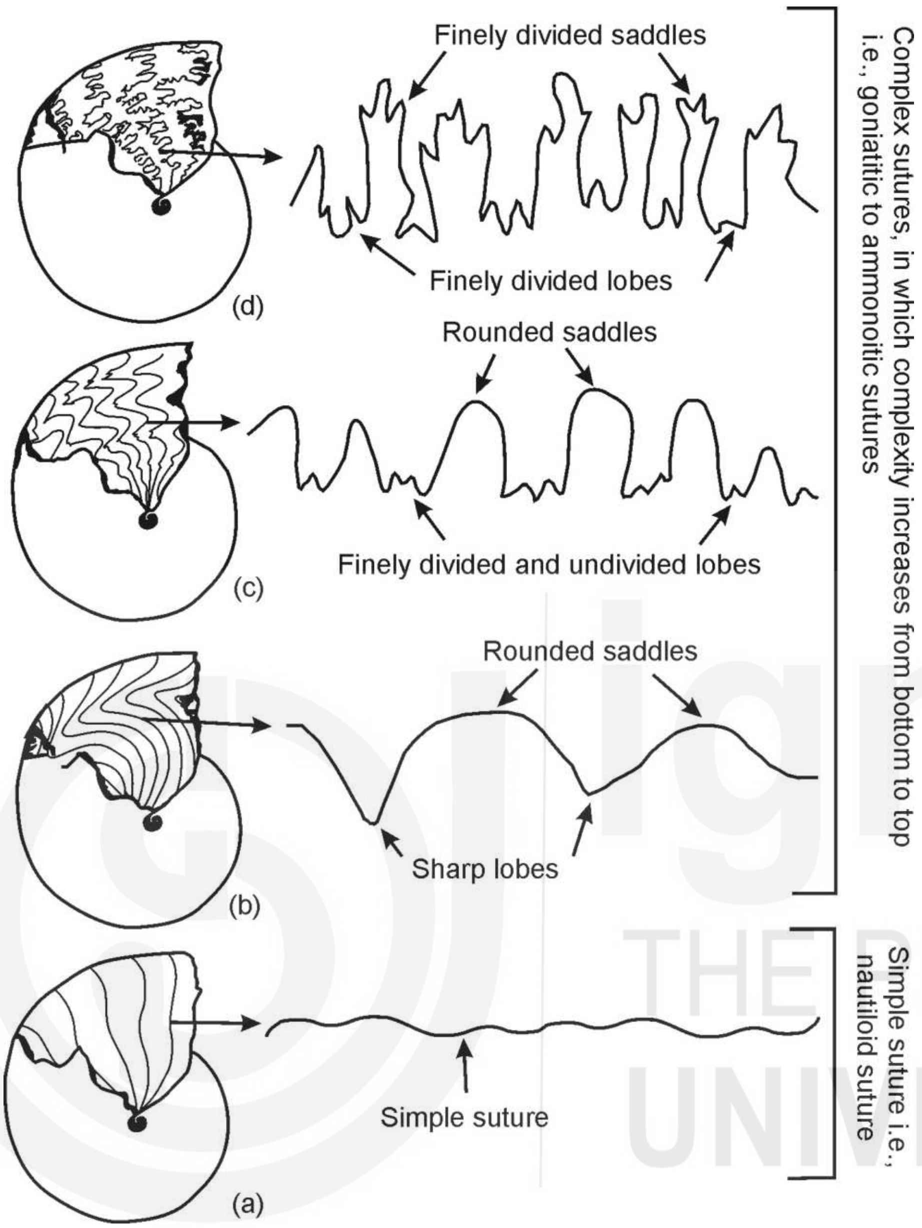

Fig. 11.8: Suture patterns in nautiloid and ammonoid cepahlopods: a) Simple suture line also known as nautiloid suture (b-d) are complex sutures, which are commonly present in ammonoids; b) Goniatitic suture; c) Ceratitic suture; and d) Ammonitic suture. (Source: Shrock and Twenhofel, 1987; Benton, and Harper, 2009)

Bactriticone is a straight conical shell (Fig. 15.9a); **gyroceratiticones** are loosely coiled shells (Fig. 15.9b); **dactylioceracones** have shells having all whorls in contact (Fig. 15.9c); **turriliticones** are eccentric coiled shells (Fig. 15.9d); **involute ammoniticones** have all whorls covered by the body whorl (Fig. 15.9e); **evolute ammoniticone** shells all the earlier formed or older whorls are visible (Fig. 15.9f). A curved or straight shell is said to be **exogastric** if the ventral side is convex (curve outside) and dorsum is curved on the inside (Fig. 15.9g). A shell is said to be **endogastric** if the dorsal side is convex (curved outside) and venter is curved on the inside (Fig. 15.9h).

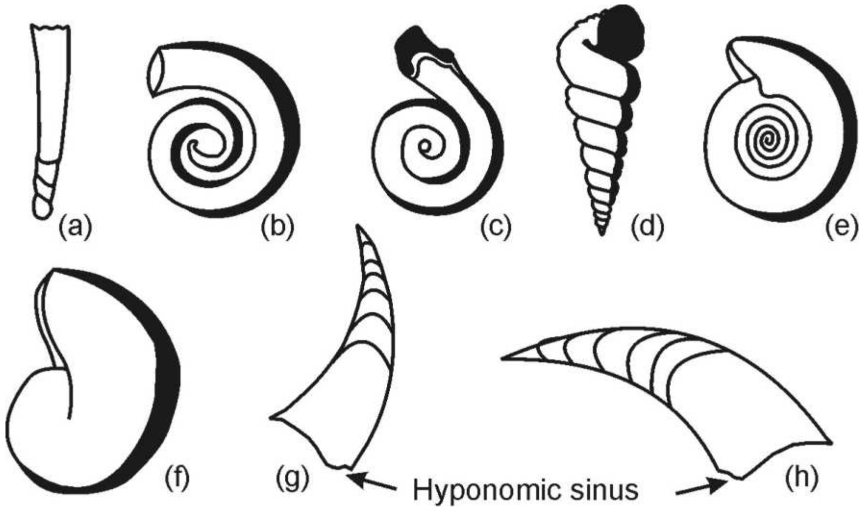

Fig. 15.9: Shells of ammonoids showing various shell forms: a) Bactriticone; b) Gyroceratiticone; c) Dactylioceracone; d) Turriliticone; e) Involute ammoniticone; f) Evolute ammoniticone; g) Exogastric; and h) Endogastric shell forms. (Source: redrawn after Shrock and Twenhofel, 1987)

Turning to the outside surface of ammonoid shells, you can see that shells show various kinds of ornamentation such as growth lines, ribs, knobs, spines, tubercles and keels. **Growth lines** are the concentric lines, in which each line represents the former position of the peristome. **Ribs** are usually radial folds that run across the whorls and **knobs** are spherical structures that extend from ribs in places. **Spines** are the projections that extend from ribs and have a pointed end. **Tubercles** are small rounded projections that normally extend from ribs and **keels** are the raised longitudinal ridges on the ventral margin.

15.4.3 Geological History

It is commonly accepted that the first ammonoids evolved probably from the bactritid cephalopods during the early Devonian. It is also proposed that bactritid must have evolved from orthoceracone nautiloids. During the early Devonian, ammonoids with goniatitic suture appeared and underwent rapid diversification in the Devonian and Carboniferous (Fig. 15.5b). They became nearly extinct at the end of the Permian. In the Carboniferous, the ammonoids with ceratitic suture appeared and they became common in Permian. They diversified during the Triassic and reached their peak during the late Triassic. Ammonoids with ammonite suture appeared at the close of Permian or at the start of Triassic. They were well-established in the Jurassic and Cretaceous periods. At the end of Cretaceous all ammonoids became extinct along with the dinosaurs (Fig. 15.5b).

During the Mesozoic, ammonoids developed a variety of shell shapes known as heteromorph ammonoids. Some shapes include uncoiled, partly uncoiled, U-bends and connected U-bends (Benton and Harper, 2009). Ammonoids were very common in the oceans of the Paleozoic and Mesozoic. Their fossil record shows their global distribution. They had a short geological range (i.e. Devonian to Cretaceous) and rapid rate of evolution. Therefore, they are considered as excellent index fossils. They make it possible to correlate sedimentary rocks in which they are found to specific geological time period.

15.5 DIFFERENCE BETWEEN NAUTILOIDS AND AMMONOIDS

If you compare the shells of nautiloids and ammonoids, you will find that both are similar in their outer or external appearance. This is because the nautiloid shell is flat and spirally coiled like the ammonids shell, so it is easy to get confused between the two. However, there are certain differences between these two groups of cephalopods, which are very significant and found on internal surfaces of their shells. These differences are given in Table 15.2.

Table 15.2: Differences between nautiloids and ammonoids.

Features	Nautiloids	Ammonoids
Coiling	Straight or spiral	Usually spiral
Siphuncle position	Central through the septa	Ventral margin of septa
Suture line	Simple	Complex (e.g., goniatitic, ceratitic and ammonitic sutures lines)
Septa	Simple	Complex
Nature of septal necks	Septal neck lies on the convex side of each septum and is projected towards the apex (protoconch) of the shell	Septal necks are directed towards the aperture of the shells

15.6 FUNCTIONAL ADAPTATIONS IN AMMONOIDS

Adaptations are a set of special characteristics of organisms that improve their functions and enable them to survive and reproduce successfully in an ecosystem. Adaptations may be categorised into functional and reproductive types. The functional adaptations include changes in morphological features of an organism that help it to survive in a better way. Reproductive adaptations help the organism to reproduce successfully. It is important to note that natural selection is the only mechanism known to cause the evolution of adaptations. For example, in most terrestrial vertebrates the skull bones are immovably joined to each other, but in snakes they are loosely joined, which enables them to swallow prey much larger than their head size. This is an adaptation that has evolved by modification of the same skull bones that are rigid in other vertebrates.

In ammonids, studies have been made to understand the function of three morphological features, namely, complex suture pattern, shell forms and complex external surface ornamentations. It is believed that the complex sutures were adaptations developed in response to shell geometry and to adjust the ambient hydrostatic pressure. The complex sutures also strengthen the shells of ammonoids and provide them efficient buoyancy control. The planispiral coiling in ammonoids helped them to move through the water quickly. Further, it indicates that the planispiral coiled ammonoids were active animals that usually lived a pelagic life style. The wider and more open shell forms of ammonoids were slow movers and lived near the ocean floor. As you know that external surface of ammonoid shells show an enormous diversity of ornamentation ranging from smooth to polished shells bearing growth lines, ribs, nodes, keels or tubercles. Many studies have proposed that the complex ornamentation on ammonoid shells were developed as a defense mechanism against the predators.

SAQ 2

a) What are ammonoids?

b) As you know that *Nautilus* is a living genus of nautiloids. Do ammonoids have any living genus?

c) List the characteristic morphological features by which you can differentiate ammonoids from nautiloids?

d) Ammonoids probably evolved from ---------------------

15.7 ACTIVITY

Illustrated below is a shell of a cephalopod mollusc. Label its various morphological parts and identify the type or subclass it belongs to.

Fig. 15.10: Shell of a cephalopod mollusk.

15.8 SUMMARY

In this unit, you have learnt the following:

- Almost all cephalopod molluscs are marine animals. They are more active, quick movers, intelligent carnivorous predators and have varied shell morphologies.
- The Class Cephalopoda consists of three subclasses, namely, Nautiloidea, Ammonoidea and Coleoidea. Of these, fossils of Nautiloidea and Ammonoidea are commonly found.
- Nautoloids are found in today's oceans and are represented by a single living genus *Nautilus,* whereas, ammonoids are all extinct.
- Body chamber, phragmocone, septa, aperture, central siphuncle, suture, septal necks, connecting rings, whorls and cameral deposits are the main morphological features of the nautiloid shells.

- Body chamber, phragmocone, septa, aperture, ventral siphuncle, goniatitic suture, ceratitic suture, ammonitic suture, septal necks, connecting rings, whorls, anaptychus and aptychus are the important morphological features of the ammonoid shells.
- Position of siphuncle, suture patterns and nature of septa are diagnostic features, by which you can differentiate nautiloids from ammonoids.
- Geological range of nautiloids is from Devonian to Present and Devonian to Cretaceous for ammonoids.
- The short geological age (i.e., Devonian to Cretaceous), rapid evolutionary history and wide geographical distribution of ammonoids make them excellent index fossils for dating the sedimentary rocks.

15.9 TERMINAL QUESTIONS

1. Write a short note on cephalopod molluscs.
2. Explain the morphology of a nautiloid shell.
3. Give a concise account of geological history of nautiloids.
4. On what basis are ammonoids differentiated from nautiloids?
5. Describe the hard part morphology of ammonoids.
6. Discuss the geological distribution of ammonoids.

15.10 REFERENCES

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15.9 FURTHER/SUGGESTED READINGS

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15.10 ANSWERS

Self Assessment Questions

1 a) Phragmocone is the chambered portion of a nautiloid shell. The chambered portion of an ammonoid shell is also called phragmocone.

b) Aragonite

c) Difference between exogastric and endogstric shells

Exogastric shell	Endogastric shell
It is curved or straight shell with convex ventral side and dorsum located inside the shell	It is curved or straight shell with dorsal side convex and venter located inside.

d) The diagnostic morphological features of nautiloids include simple septa and suture, and centrally placed siphuncle.

2 a) Ammonoids are an extinct group of marine cephalopod molluscs. They belong to the Subclass Ammonidea and Class Cephalopoda of the Phylum Mollusca. They constitute the largest and one of the most important subclasses of cephalopods and lived from early Devonian to late Cretaceous. It is generally accepted that ammonoids were evolved from the genus *Bactrites.* The ammonoids shells are either tightly coiled on a single plane (i.e., planisprial) or open helical and irregularly coiled as well as straight and much similar to the shells of nautiloids in external surface morphology.

b) Yes, *Nautilus* is a living genus of nautiloids. The ammonoids, appeared in early Devonian and became extinct at the end of Cretaceous. Hence, they do not have any living representative. In fact, their fossils are very useful for startigraphic correlation.

c) The external surface appearance of both ammonoids and nautloids has remarkable similarity. However, there are some characteristic morphological features, which are found inside the shells of ammonoids on the basis of which we can differentiate ammonoids from nautiloids. These features are ventral position of siphuncle, complex pattern of suture (e.g., goniatitic, ceratitic and ammonitic) lines and complex nature of septa.

d) *Bactrites*

Terminal Questions

1. Refer to section 15.2.
2. Refer to subsection 15.3.2.
3. Refer to subsection 15.3.3.

4. Refer to section 15.5.
5. Refer to subsection 15.4.2.
6. Refer to subsection 15.4.3.

UNIT 16

TRILOBITES AND ECHINODERMS

Structure

16.1 INTRODUCTION

In units 13 to 15 of this block, we have discussed some important groups of invertebrate fossils, namely corals, brachiopods, bivalves, gastropods and cephalopods. They appeared in the Cambrian and are still alive today except ammonoid cephalopods. Ammonoid cephalopods are an extinct group of marine molluscs, which first appeared in the Devonian and became extinct at the end of the Cretaceous. They are now used as index fossils for dating of sedimentary rocks. *Lingula* and *Nautilus* are living fossils of brachiopods and nautiloid cephalopods, respectively, which provide living samples to the palaeontologists for understanding the soft parts anatomy of their fossil relatives.

We shall now turn to the remaining two major groups of invertebrates, which are trilobites and echinoderms. Like ammonoids, trilobites are also extinct, but an important fossil group for palaeontologists. Echinoderms, however, have living representatives and are also entirely marine. They have a rigid skeleton and their two classes, namely, echinoids and crinoids are useful for palaeontological study. In this unit, we will discuss the morphology, systematic and geological history of trilobites, echinoids and crinoids.

Expected Learning Outcomes

After reading this unit, you should be able to:

- ❖ define trilobites and echinoderms;
- ❖ describe the skeletal morphology of trilobites;
- ❖ classify echinoderms;
- ❖ describe the test morphology of echinoids and crinoids; and
- ❖ discuss the geological history of trilobites, echinoids and crinoids.

16.2 TRILOBITES

Trilobites are an extinct group that belongs to a very large phylum of invertebrates called Arthropoda. It is morphologically a diverse group and includes a great variety of invertebrates such as insects, spiders, scorpions, centipedes, millipedes, crabs, ostracods and their fossil relatives like eurypterids and trilobites. This phylum alone constitutes about 40% of total life on the planet Earth. Arthropods are found everywhere, for example, in sea water, freshwater and on land. They have segmented bodies with six or more jointed legs and a hard protective external skeleton (i.e., exo-skeleton), which needs to moult or shed as the animal grows. The exo-skeleton of arthropods is composed of organic material chitin and proteins. Arthropods are generally small-sized with many forms less than 1 cm long, but a few others are over 3.2 m long.

16.2.1 What are Trilobites?

Trilobites are an extinct group of marine Palaeozoic arthropods. They belong to the Class Trilobita and the Subphylum Trilobitomorpha. The name Trilobite is derived from the two Greek words **Tri** meaning three and **Lobos** meaning lobes, referring to three lobes or trilobation of trilobite's skeleton. It is believed that they are the primitive arthropods. Trilobites are one of the most diverse classes of extinct invertebrates, comprising more than 20,000 species. Like other arthropods, the exo-skeleton of trilobites has numerous segments and paired appendages (Fig. 16.1). It is mainly chitinous in composition and is made up of three lobes. The size range of average trilobites is 50 to 75 mm in length. The smallest known trilobite is about 1 mm long, while the longest known is 70 cm.

Fig. 16.1: Photographs of trilobites: a) Simple photograph; and b) High resolution photograph. (Source: Dr. S.K. Pracha for b)

16.2.2 Systematic Palaeontology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Arthropoda
Subphylum	Trilobitomorpha
Class	Trilobita
Order	Agnostida
	Polymerida

Important genera of trilobites: *Olenellus*, *Agnostus*, *Phacops*, *Paradoxides*, *Redlichia*, *Olenus*, *Illaenus* and *Calymene*.

Do you know?

Trilobites leave their exo-skeleton to be fossilised, not only once when they died, but also at their numerous stages of moulting, which provided plentiful skeletons for fossilisation. Molting is a process of discarding an old skeleton and developing a new one when an animal grows.

16.2.3 Morphology

Trilobites had a hard external skeleton composed of organic material chitin which further strengthened with crystals of calcite. Since trilobite is an extinct group of animals, very little is known about its soft part morphology. It may be noted that the dorsal side (also known as dorsal shield) of a trilobite is the only part of its exo-skeleton which is commonly preserved as fossils. Therefore, we will focus mainly on the dorsal morphology of trilobites.

The exo-skeleton of trilobites is divisible into three parts both longitudinally and transversely. In longitudinal position or along the body, the skeleton is divided into one axial lobe and two pleural or lateral lobes. The central lobe is known as **axial lobe** (Fig. 16.2a) where as **pleural lobes** are situated on either side of the skeleton. The pleural lobe on the right side is described as **right pleural lobe** and that on the left side is **left pleural lobe** (Fig. 16.2a).

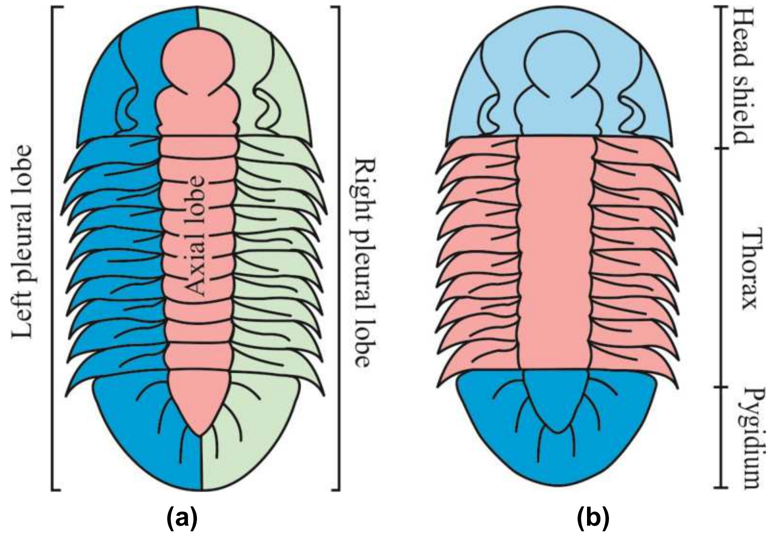

Fig. 16.2: Trilobation of a trilobite skeleton: a) Longitudinal; and b) Transversal.

The exo-skeleton of trilobites is also divided transversely or across the body into following three parts (Fig. 16.2b): -

i. Cephalon or head shield

ii. Thorax

iii. Pygidium or tail

The cephalon and pygidium which lie on anterior and posterior margins of the skeleton, respectively, have fused segments. On the other hand, thorax that lies between cephalon and pygidium has numerous unfused segments which are attached to each other (Fig. 16.2b). Let us now discuss each part of a trilobite skeleton in the same order as given above one by one in the following section.

Orientation of trilobite skeleton: In a trilobite skeleton, the commonly preserved surface is the **dorsal side**, which is the upper or back side of the animal; the underside or belly portion is referred to as **ventral side**; cephalon region is known as its **anterior side** and pygidium end is the **posterior side**.

i. **Cephalon or Head Shield**

The dorsal part of the trilobite skeleton that covers the head is known as **cephalon** or **head shield**. It lies on the anterior margin of the skeleton, has a semi-circular outline and is formed by fusion of five to seven segments. It is made up of glabella and cheeks. The raised axial (central) area of cephalon is called **glabella**, whereas the portion of cephalon that surrounds glabella comprises **cheeks** (Fig. 16.3). There are two axial furrows which separate glabella from cheeks. Glabella is divided by short transverse furrows into an **anterior lobe** and **lateral glabellar lobes**. **Transverse** or **lateral furrows** are basically the segments present on the left and right margins of the glabella. In some forms, transverse furrows do not join each other across the median line and form a **median lobe**. The last fused segment of glabella close to the posterior margin of cephalon is known as **occipital lobe** and is separated from the rest of glabella by an **occipital furrow** (Fig. 16.3). It may be noted that **cheeks** comprise the portions on either side of the glabella and are divided along a facial suture into free cheek and fixed cheek. Some trilobites were eyeless and others had a pair of compound eyes. The compound eyes situate at the outer edges of the fixed cheeks on both sides of the glabella, adjacent to the facial sutures.

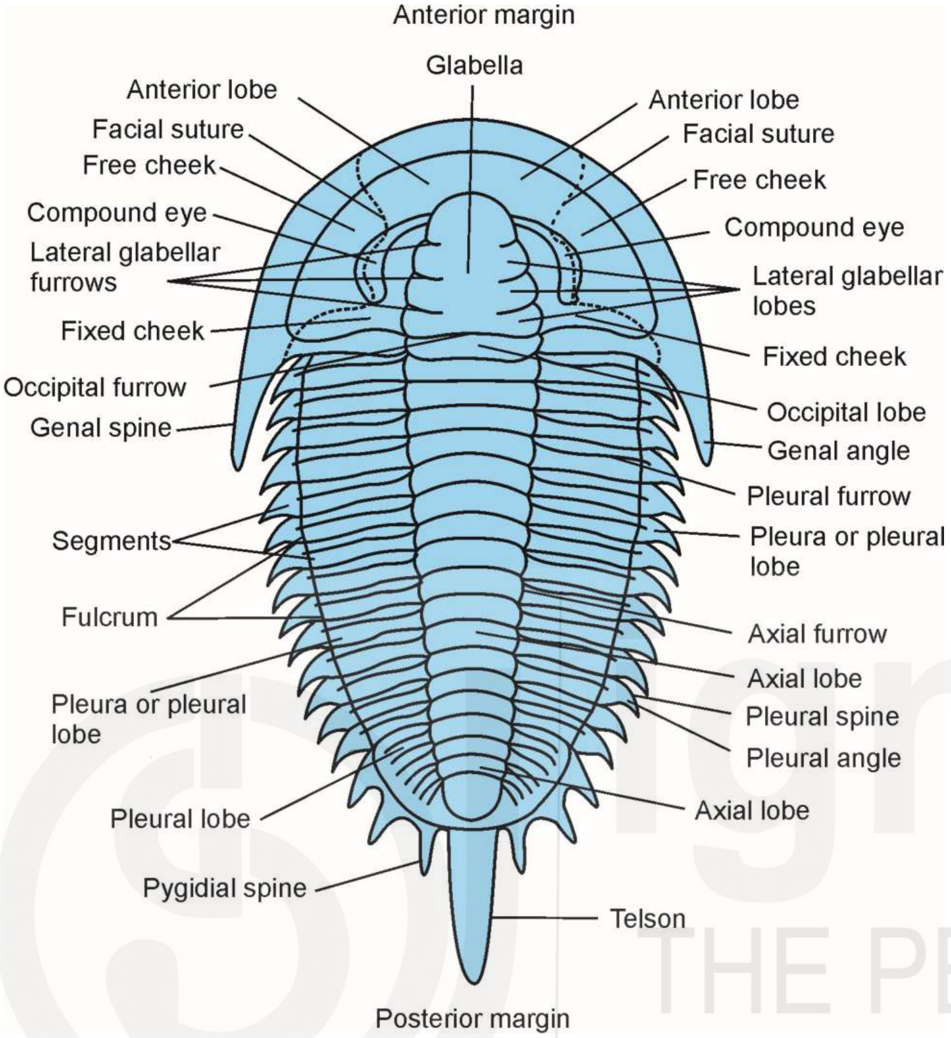

Fig. 16.3: Line drawing of a trilobite showing the various morphological features. (Source: simplified after, Shrock and Twenhofel, 1987; Moore et al., 1997; Benton and Harper, 2009)

Facial sutures are lines of weakness present on the cheeks. The part of cheek which is in contact with glabella is termed as **fixed cheek** and the one on the outer side is known as **free cheek**. The combined central portion of cephalon bounded by glabella and two fixed cheeks (on both sides of the glabella) is known as **cranidium**. The angle formed by meeting the lateral and posterior margins of cephalon is known as **genal angle**. In some forms, genal angle is very acute and produces a posterior lateral extension in the form of a spine, which is described as a **genal spine** (Fig.16.3). It is interesting to note that trilobites commonly split their exo-skeleton during molting along the facial sutures that can be divided into four types with respect to their position at cephalon's edge relative to the genal angle as given below and shown in Fig 16.4.

a. Proparian Facial Suture: It cuts margin in front of the genal angle.

b. Opisthoparian Facial Suture: It cuts margin at the genal angle.

c. Gonatoparian Facial Suture: This suture cuts margin behind the genal angle.

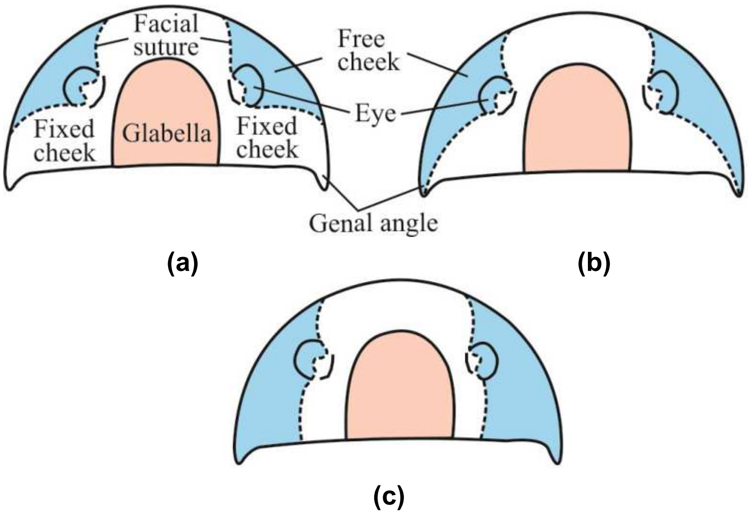

Fig. 16.4: Cephalons of trilobites showing various types of facial sutures: a) Proparian; b) Opisthoparian; and c) Gonatoparian. (Source: simplified after Nield and Tucker, 1985)

ii. **Thorax**

Thorax is the central portion of a trilobite's skeleton, which lies in between cephalon and pygidium. It is made up of a series of nearly identical segments, which are usually two to forty two in number and not fused together. The segments are movable. It may be noted that transversely, each segment is a single piece, but it is easily divisible into three lobes such as an axial lobe and two pleural lobes by two **axial furrows**. The median or central portion of each segment is known as **axial lobe** and its lateral lobes lying on either side of the axial lobe are termed as **pleura** or **pleural lobes** (singular, pleuron) (Fig. 16.3). Each pleuron at some distance from the axial lobe is curved forming a **fulcrum**. The lateral end of each pleuron may be rounded or produced. If the end is rounded then it gives rise to an angle known as **pleural angle**; on the other, if it is produced then it is termed as **pleural spine**. The horizontal grooves present on external surfaces of segments are known as **pleural furrows** (Fig. 16.3).

iii. **Pygidium**

Pygidium is a tail piece, which lies at the posterior margin of trilobite. It is triangular to semi-triangular in shape and composed of a variable number of segments, which are fused together, immovable and may be one to thirty in number. Pygidium may be larger or smaller than the cephalon. Like the segments of thorax, it is also divided into an axial lobe and two pleural lobes. In some forms, the posterior end of pygidium has an extension of an axial spine, which is termed as **telson**. The spines occurring in the pygidium region are known as **pygidial spines** (Fig.16.3).

Based on the size of pygidium, trilobites may be defined as given below and shown in Fig. 12.5:

a. Micropygous: When pygidium is small.

b. Macropygous: When pygidium is larger than cephalon.

c. Isopygous: Pygidium and cephalon are equal in size.

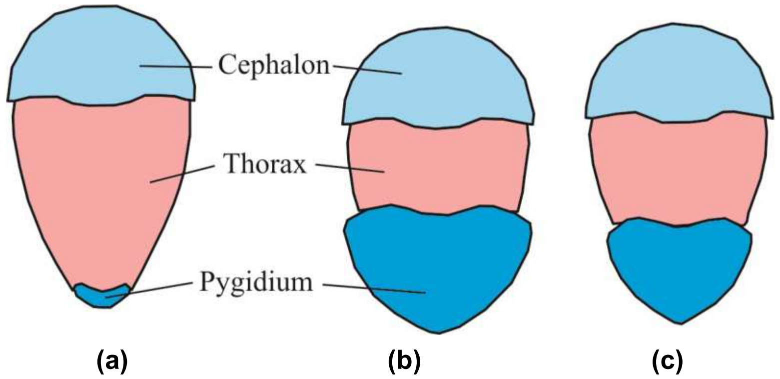

Fig. 16.5: Schematics of trilobites showing: a) Micropygous; b) Macropygous; and c) Isopygous trilobites.

Key morphological features of trilobites: cephalon or head shield, thorax, pygidium or tail, glabella, cheeks, genal angle, genal spine, axial furrows, pleural angle, pleural spine, pleural lobes and telson.

16.2.4 Geological History

Trilobites first appeared in the early Cambrian. During the middle Cambrian and Ordovician, they underwent a dramatic diversification, which led to the appearance of many new forms. During these periods, *Olenellus*, *Agnostus*, *Paradoxides*, *Redlichia*, *Olenus*, *Illaenus* and *Calymene* were the common genera of trilobites. After the end of Ordovician, trilobites began to decline during Silurian, Devonian and Carboniferous and completely disappeared at the end of Permian (Fig. 16.6).

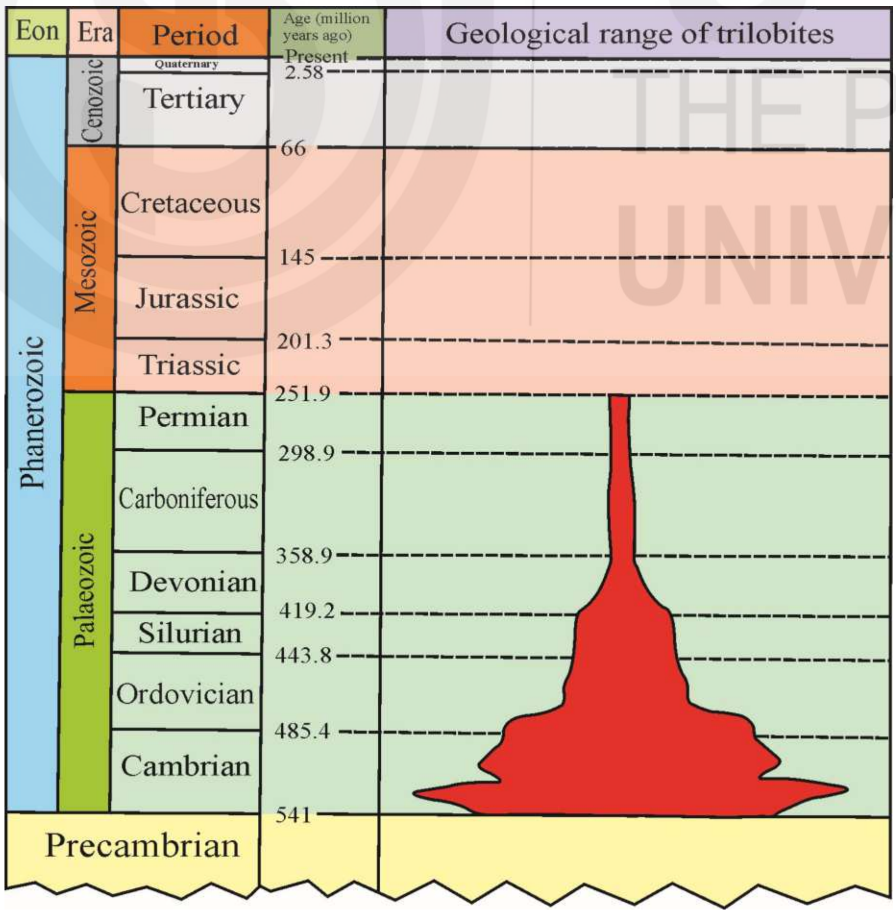

Fig. 16.6: Stratigraphic distribution of trilobites. Width of the column represents the abundance of trilobites in the Palaeozoic. (Source: simplified after Milsom and Rigby, 2010)

It is reasonable to conclude that trilobites were a dominant group of invertebrates during the early Palaeozoic, as maximum numbers of species were present in the Cambrian and Ordovician. After that they became less dominant and vanished at the close of Palaeozoic.

SAQ 1

a) Trilobites were ……… animals.

i) Fresh water ii) Marine iii) Terrestrial

b) Describe transverse and longitudinal divisions of a trilobite skeleton.

c) What is a cephalon?

d) Trilobites belong to the phylum:

i) Echinodermata ii) Mollusca iii) Arthropoda iv) Brachiopoda

e) Geological age range of trilobites is:

i) Cambrian – Cretaceous ii) Cambrian – Carboniferous iii) Cambrian – Permian

16.3 ECHINODERMS

Like cephalopod molluscs, echinoderms are exclusively marine animals and did not occur on land or in fresh water. They form a large and successful phylum of invertebrates. The Phylum Echinodermata (e-KI-no-der-MA-ta) includes living forms such as sea urchins (echinoids), starfish, brittle stars, sea lilies (crinoids), sea cucumbers and extinct forms like cystoids and blastoids. The name Echinodermata is derived from two Greek words **Echinos** meaning spiny and **Derma** meaning skin, referring the spiny-skinned nature of animals. All echinoderms have a very different body plan, which stands apart from other invertebrate groups. The echinoderms are spiny-skinned animals and commonly possess the following three unique body features:

- rigid mesodermal skeleton made of interlocking plates and spines of calcite,
- five-fold or pentameral radial symmetry in adults (Fig. 16.7), which may be superimposed by a bilateral symmetry, and
- water vascular system used for locomotion, sensing and food gathering.

16.7: Star-fish showing five-fold or pentameral radial symmetry. (Source: Dr. S.N. Kundal)

Phylum Echinodermata is divisible into two groups on the basis of their habitat.

1. **Eleutherozoans**: They are characterised by the absence of stem and are free and mobile.

   Example – echinoids.

2. **Pelmatozoans**: They have a stem that is attached to the ocean floor. Typical

   Example – crinoids.

It may be noted that echinoids and crinoids are the most significant classes of echinoderms palaeontologically. Therefore, we will discuss these two classes in succeeding sections of this unit.

16.4 ECHINOIDS

The echinoids are marine animals and belong to the Class Echinoidea. The name Echinoidea is derived from two Greek words **Echinos** meaning spines and **Oidea** meaning test, signifying the test covered with spines. They include sea urchins, heart urchins and sand dollars. The soft parts of the animal are enclosed inside a rigid calcareous skeleton, which is composed of many closely fitting plates of calcite. The skeleton of echinoids is also known as **test** (Fig. 16.8). The tests may be spherical, globular, discoidal or heart-shaped and covered with spines. Most of the echinoids show pentameral (five-fold) radial symmetry whereas a few others show bilateral symmetry. The tests of echinoids range in size from 3 to 10 cm in diameter or length.

Fig. 16.8: Test of an echinoid. (Source: Dr. V.K. Sharma, Govt. Holkar Science College, Indore)

Echinoids can be divided into two main groups: regular and irregular.

- **Regular or Endocyclic Echinoids**: They have five-fold (pentameral) radial symmetry and spherical to circular body.
- **Irregular or Exocyclic Echinoids**: They have bilateral symmetry and a heart-shaped body.

16.4.1 Systematic Palaeonotology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Echinodermata

Class	Echinoidea
Order	Regularia
	Irregularia

Common genera of echinoids: *Echinus, Hemiaster, Micraster, Cidaris, Cyphosoma, Discoidea, Holaster* and *Conulus*.

16.4.2 Morphology

The tests of most of the echinoids are hemispherical in shape and covered with spines. A typical test has two poles, namely, oral and aboral. The lower side of the test is known as **oral** pole and it is normally flattened. On the other hand, the upper side, which is usually convex, is termed as **aboral** pole (Fig. 16.9). The mouth of the animal is situated at the oral pole and anus at the aboral pole. It is important to note that the terms oral and aboral are used to describe the position of poles of an echinoid's test instead of using ventral and dorsal. The side of the pole where the mouth lies is known as the oral (or ventral) side and the opposite side where anus lies is referred to as aboral (or dorsal) side.

A test consists of many interlocking calcitic plates. The plates surrounding the mouth are collectively described as **peristome**, whereas those encircling the anus are termed as **periproct**. Morphologically, a test of an echinoid may be divided into three parts:

I. Apical system or disc
II. Corona
III. Peristome

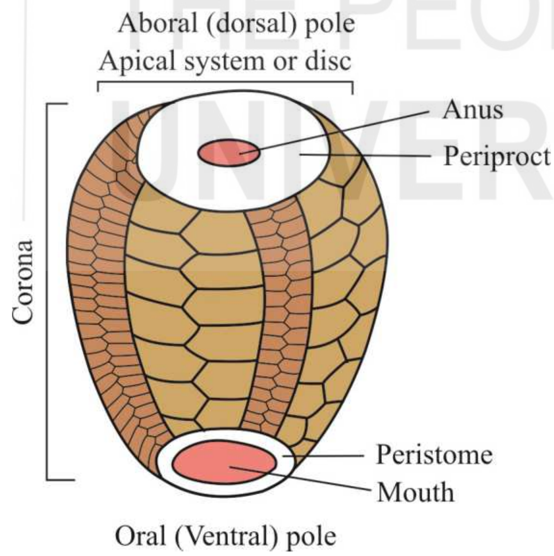

Fig. 16.9: Schematic of an echinoid showing the main divisions of the test.

I. **Apical System or Apical Disc**: It is a small area lying at the apex or summit of the aboral surface (Fig. 16.9). It is composed of ten plates which form a ring around the periproct. Out of these ten plates, five are known as **genital plates** and the rest are **ocular plates**. The genital plates are larger and hexagonal in outline and form the inner part of the ring. One of the genital plates is larger than other genital plates, has many small pores, and is known as **madreporite** or **porous plate** (Fig. 16.10). The ocular plates are smaller than genital plates and triangular to pentagonal in outline. Each of the genital and ocular plates is perforated by a pore. It may be noted that to complete a ring of ten plates around the periproct, both genital and ocular plates are attached alternatively with each other and in many cases ocular plates partially form the outer part of the ring. In such cases, ocular plates do not touch the periproct and this condition of the test is termed as **exsert** (Fig. 16.11a). However, in other cases, ocular plates separate the genital plates and touch the periproct, this condition is known as **insert** (Fig. 16.11b). It may be noted that in irregular echinoids, the apical disc is small and does not encircle the periproct.

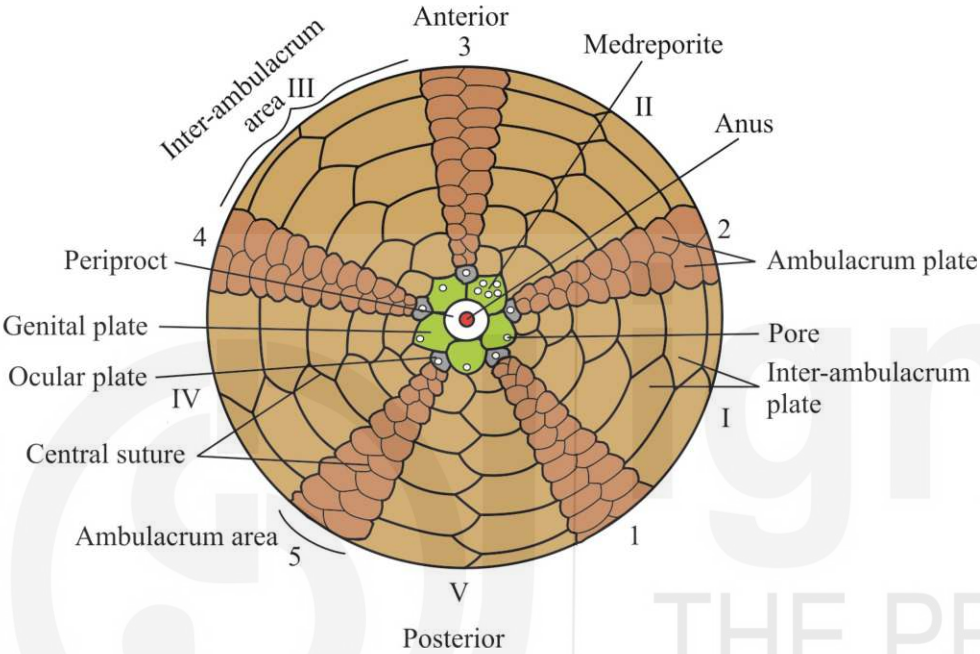

Fig. 16.10: Line drawing of the aboral view of an echinoid showing the apical system. Note: 1 to 5 are ambulacral plates and I to V are the inter-ambulacral plates.

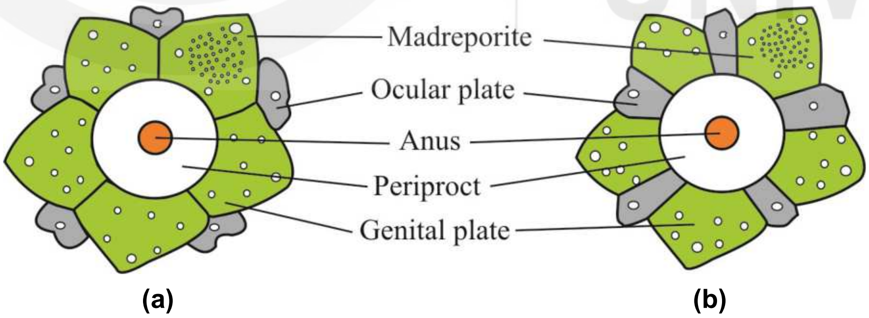

Fig.16.11: View of the apical systems of echinoids showing: a) exsert; and b) insert tests.

II. **Corona**: It is the main part of the test, which starts from the apical disc and ends at the peristome. It is composed of ten pairs of columns of plates, which are collectively described as the **coronal plates**. Out of these ten pairs, five double columns which carry tube feet are known as **ambulacral plates** and the other five with no tube feet are termed as the **inter-ambulacral plates** (Fig. 16.10). Tube feet are small fleshy suckers which come up from the water-vascular system of the animal through pores in the test to capture food. The five double columns of ambulacral plates are separated by five double columns of inter-ambulacral plates, in which each double column is described as an **area**. The area of ambulacral plate is termed **ambulacral area** and area of an inter-ambulacral plate is known as **inter-ambulacral area** (Fig. 16.10). In each area, plates are fixed alternatively. Each pair of both ambulacral and inter-ambulacral columns is composed of two rows of elongated plates, which meet along a central suture in a zig-zag pattern. The ambulacral plates are small in size, larger in number, perforated by pores and in contact with ocular plates of the apical disc. The inter-ambulacral plates are larger in size, small in number as compared to ambulacral plates, bear spines and terminate against the genital plates of the apical disc. Ambulacral plates are said to be **simple ambulacral plates** if they are made up of only a single piece and said to be **compound plates** when they are made up of two or more smaller plates. In some form of echinoids, the ambulacral plates look-like a petal and all ambulacral plates together show a flower-like structure, which is termed as **petaloid**. It should be noted that ambulacral and inter-ambulacral plates lie alternatively and run vertically between periproct and peristome. The coronal plates may be covered by spines and tubercles. Tests of regular ehinoids possess the larger spines and tubercles whereas smaller spines and tubercles are found on tests of irregular ehinoids.

III. **Peristome**: It lies on the oral side of the test. Peristome is an opening in the test associated with the mouth and is circular to polygonal in outline (Fig. 16.12). The mouth of an animal occurs at the centre of the peristome and represents a region where ambulacral and inter-ambulacral plates converge. It would be of interest to you to note that both periproct (an opening associated with anus) and peristome are generally not preserved in fossils.

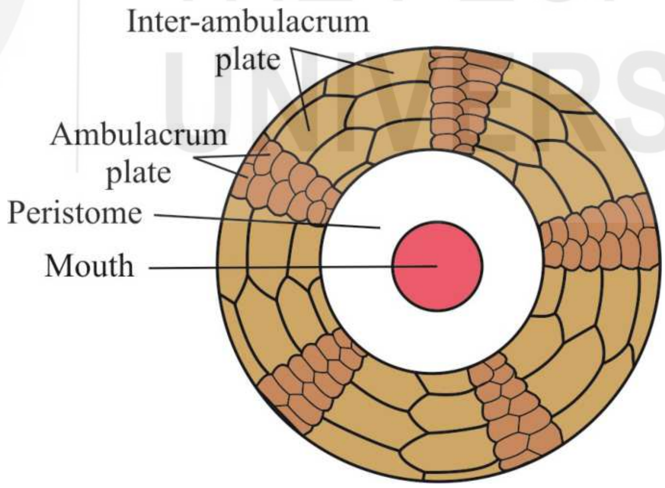

Fig. 16.12: Oral view of an echinoid showing the peristome.

Key morphological features of echinoids: genital plates, ocular plates, madreporite, ambulacral plates, inter- ambulacral plates, periproct and peristome.

16.4.3 Geological History

The earliest echinoids are known from the Ordovician. They diversified during the Ordovician, Silurian, Devonian and Permian periods of the Palaeozoic era During the Carboniferous, they suffered considerable loss in their diversity

(Fig. 12.13). However, they did not emerge as a dominant group of echinoderms during the Palaeozoic times. The complete fossils of echinoids from the Palaeozoic are rare and we may find their fragmentary remains consisting of isolated spines and pieces of test. It is interesting to note that the majority of the Palaeozoic echinoids belong to the order Regularia.

In Mesozoic, echinoids underwent a dramatic diversification and became a dominant group of the phylum Echinodermata. Irregular echinoids first appeared in the Mesozoic and most of the Mesozoic echinoids belong to order Irregularia. During the Mesozoic, echinoids emerged as a significant element of marine fauna. During the Cenozoic they became less important but they diversified during the late Cenozoic. In Cenozoic, irregular echinoids became more important while the regular echinoids became less abundant. At present there are more than 900 species of echinoids living in various oceans and seas. Echinoids are entirely marine and their fossils are good indicators of marine environment.

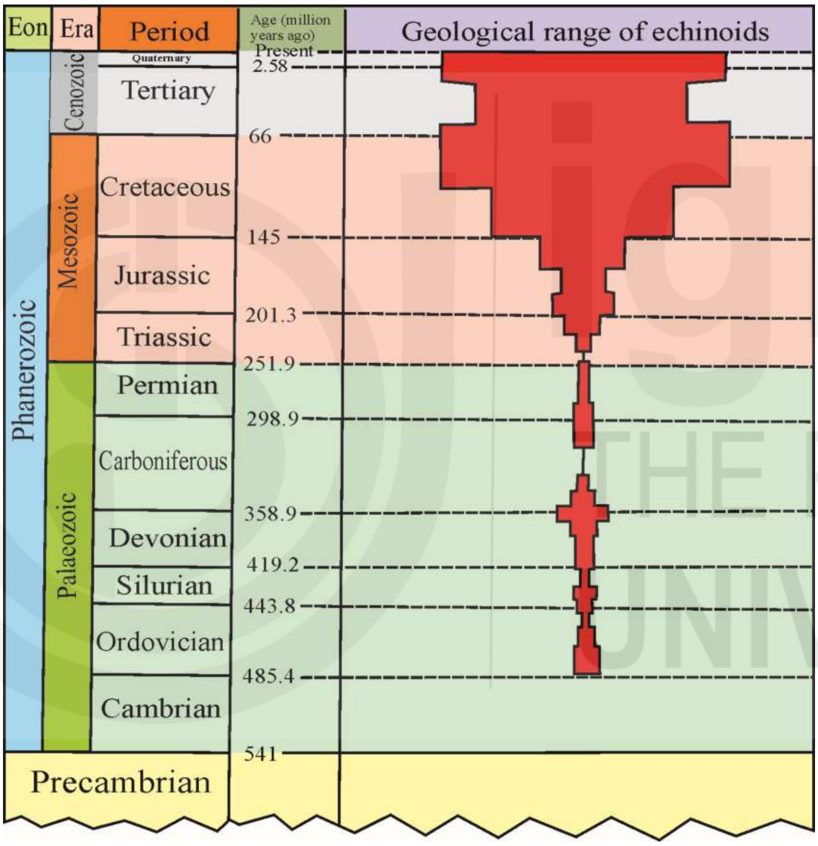

Fig. 16.13: Stratigraphic distribution of echinoids. Width of column represents the abundance of echinoids in a particular period/era. (source: simplified after Jones, 2011)

SAQ 2

a) What are the three characteristic features of echinoderms?

b) Write three parts of an echinoid test.

c) Apical disc of the echinoid is made up of ---------------------- plates.

d) Echinoderms live:

i) in fresh water ii) in ocean iii) on land

e) Give the geological age range of echinoids.

16.5 CRINOIDS

Crinoids are popularly known as sea lilies because older forms look more like plants than animals. The modern forms are known as feather stars. They are, indeed, animals and closely related to other echinoderms particularly sea urchins and starfish. The name Crinoid is derived from two Greek words *Krinoni* meaning lily and *Oid* meaning like, referring to lily-like appearance of the animal. Crinoids belong to the Class Crinoidea of the Phylum Echinodermata. They are generally flower-like animals, which occur mostly attached to the sea bottom by means of a stem, for example, as sea lilies whereas others are stemless movable forms, for example, feather stars. Most of the living or modern crinoids are stemless feather stars. The sea lilies occur in the deep ocean whereas feather stars occupy shallow waters. It may be noted that the stemless crinoids are also attached to the sea bed by a stem during their early growth stage, but in the adult stage they break their stems from the sea bed and become free-swimming forms. They possess an attachment mechanism known as **cirri** so that whenever required they could attach themselves temporarily to the sea bed.

Crinoids possess pentameral (five-fold) symmetry and their body consists of a stem, a calyx and movable arms. The body size of crinoids ranges from 1 mm to 18 m in length. Most living stemless crinoids are less than 25 cm in length (Moore et al., 1997).

16.5.1 Systematic Palaeonotology

Kingdom	Animalia
Subkingdom	Metazoa
Phylum	Echinodermata
Class	Crinoidea
Subclass	Inadunata
	Flexibilia
	Camerata
	Articulata

Key genera of crinoids: *Antedon, Dendrocrinus, Merocrinus, Thenarocrinus, Cupulocrinus, Encrinus, Apiocrinites* and *Erisocrinus*.

16.5.2 Morphology

The body of a typical crinoid is composed of numerous calcite plates held together by means of muscle and ligaments. It is divided into three parts from bottom to top:

- Stem
- Calyx
- Arms

I. **Stem**: Stem is a more or less flexible part of the animal where its lower end is commonly attached to the ocean floor and the upper end is fixed to the calyx. It is made up of disc-shaped calcareous columnar plates, which are arranged usually in a single series and termed as **ossicles** or **columnals** (Fig. 16.14). All columnal plates have a central canal and these canals together form an **axial canal**. The axial canal is circular in outline, but in some forms it shows pentameral symmetry. Most columnal plates of the stem are marked by grooves, which hold the columnal plates together tightly and produce a rigid stem. While in other cases, columnal plates have a central ridge, which joins the plates loosely and produces a flexible stem.

The root-like structure, which fixes the lower part of the stem to the ocean floor permanently, is known as **holdfast**. The free-swimming forms of crinoids can attach temporarily their stems to the ocean floor by a root-like structure known as **cirri**.

II. **Calyx**: It is located between the stem and arms, and houses the vital organs of animal-like digestive and reproductive organs. It is generally made up of two rings of calcareous plates, namely, basals and radials (Fig. 16.14). **Basal plates** are five in number and located in the region where the top most part of the stem meets the lowermost part of calyx. In a few crinoids, three extra plates occur between the stem and basal plates, which are termed as **infra-basals**. **Radial plates** are also five in number and are situated above the basal plates. On the basis of basals, radials and infra-basals crinoids are morphologically classified into:

- **Monocyclic crinoids**: These possess only basal and radials.
- **Dicyclic crinoids**: These possess the basals, radials and infra-basals.

It is reasonable to note that the part of the calyx above the arm bases is the ventral or oral surface and is known as **tegmen**. The part of the calyx below the arm bases is the dorsal or aboral surface. The mouth of an animal is situated in the centre of the ventral or oral surface and anus is located peripheral to it. A combination of calyx and the arms is known as the **crown**.

III. **Arms**: Arms are the topmost part of the body. They are present on all crinoids, radiating off from the radials of the calyx. The arms, usually five in number or multiples of five, are a more flexible feature of the crinoid body. Hence, they are free to move in any direction. Each arm is made up of a number of calcareous ossicles or plates known as **brachial** or **arm** (Fig. 16.14). The brachial plates may be either in a single row or in two rows and are described as **uni-serial** and **bi-serial**, respectively. The brachials may bear fine unbranched extensions like the leaves of a fern known as **pinnules**, which give feathery appearance to the arms. It may be noted that the main function of arms is to capture the food particles and supply them to the mouth, which is located in the centre of calyx. **Anal tube** is an elongate chimney-like extension from the centre of tegmen. It has an anal opening at the top.

Key morphological features of crinoids: Stem calyx, arms, columnals, axial canal, holdfast, cirri, basals, radials, pinnules and anal tube.

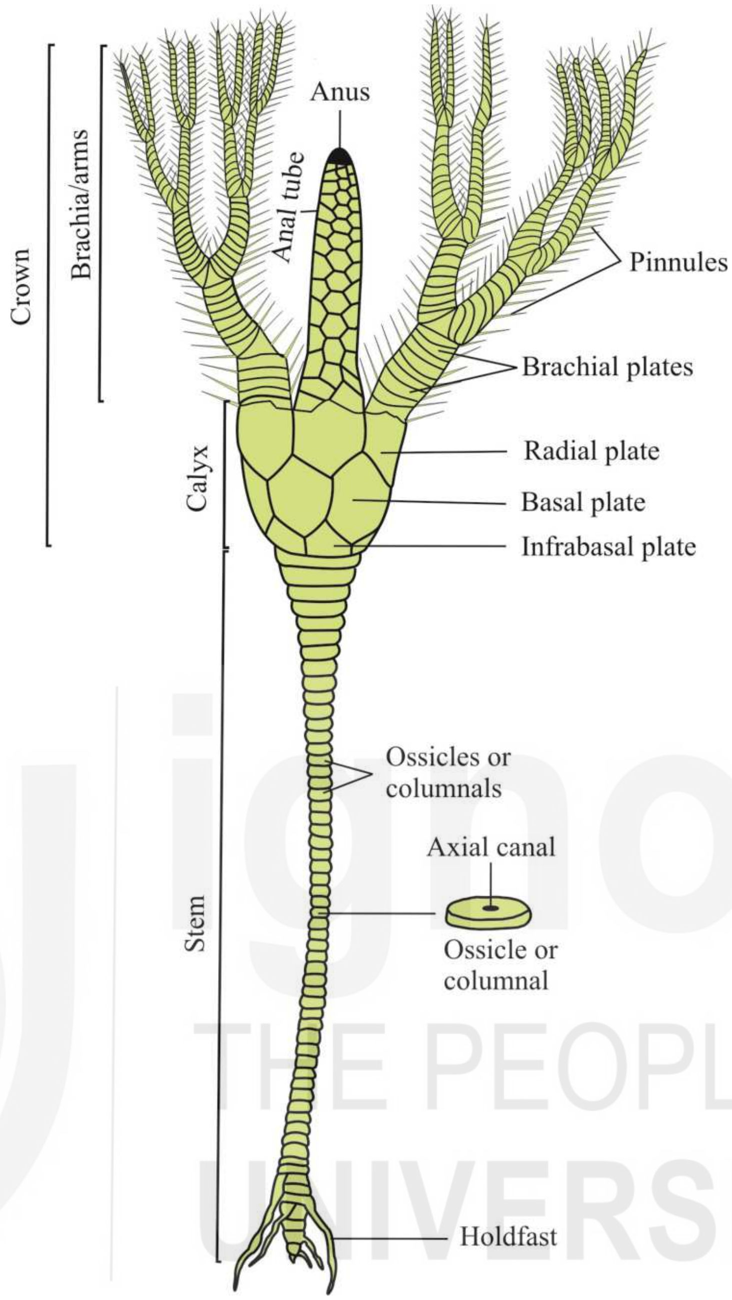

Fig. 16.14: Line drawing of a crinoid showing its basic morphological characters. (Source: modified after Nield, 1987)

16.5.3 Geological History

Crinoids first appeared in the Ordovician. They diversified during the Ordovician, Silurian, Devonian, Carboniferous and Permian of the Palaeozoic. However, they also sustained a significant loss in diversity during the late Devonian and late Permian (Fig. 16.15). A majority of crinoids appeared in the Paleozoic. Most of the Palaeozoic crinoids were permanently fixed to the ocean floor by stems and free-swimming forms did not appear in this era. Crinoids formed an important component of marine fauna from Ordovician to Permian in the Palaeozoic era. At the end of Palaeozoic, most crinoids died out and only a single form survived into the Mesozoic.

The stemless crinoids first appeared in the Triassic. Both stemed and stemless crinoids were present in the Mesozoic, but they did not emerge as a dominant group of echinoderms. From Mesozoic to present, crinoids have continuously been persisting in marine environments and stemless forms have increased their dominance over the stemed crinoids.

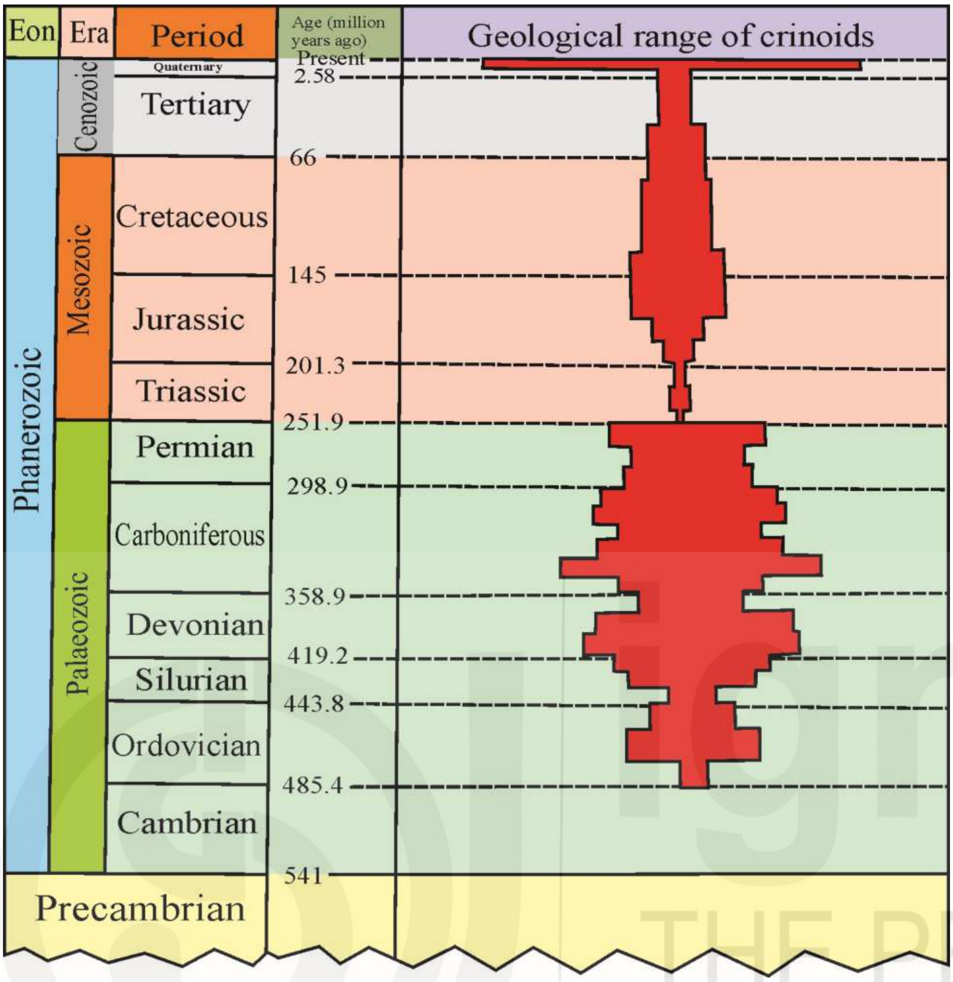

Fig. 16.15: Stratigraphic distribution of crinoids. Width of column represents the abundance of crinoids in a particular period/era. (Source: simplified after Jones, 2011)

SAQ 3

a) Echinoids and crinoids belong to the phylum:

a) Brachiopoda b) Mollusca c) Echinodermata d) Echinoidea

b) Crinoids are:

a) Invertebrates b) Plants c) Vertebrates

c) List the major hard parts of a crinoid's body.

d) What is the geological age range of crinoids?

16.6 ACTIVITY

In subsection 16.2.3, you have learnt about the various morphological features of trilobites. Below is a line drawing of a trilobite (Fig. 16.16). Try to identify the following morphological features: cephalon or head shield, thorax, pygidium or tail, glabella, cheeks, facial suture, axial furrows, occipital lobe, pleural furrow, pleural lobes and telson, and label them.

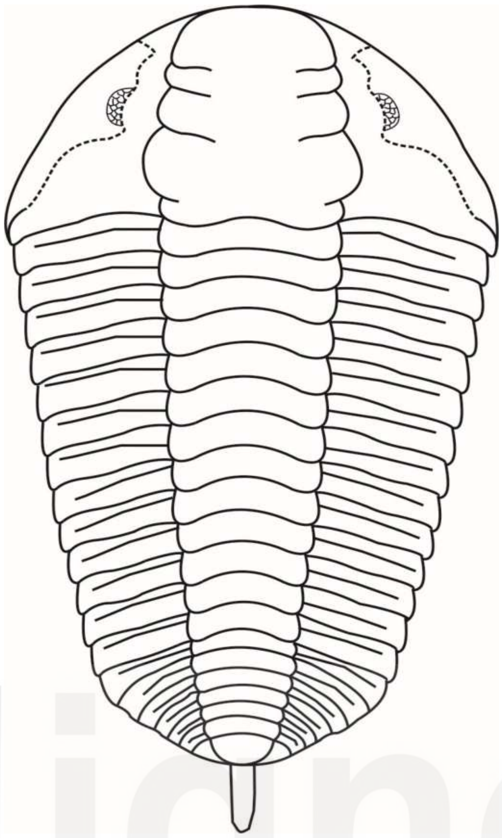

Fig. 16.16: Line drawing of a trilobite.

16.7 SUMMARY

Let us quickly summarise what you have read in this unit.

- Trilobites and echinoderms were/are exclusively marine animals.
- Trilobite had an exo-skeleton, which is easily divisible into three parts – cephalon or head shield, thorax and pygidium or tail.
- Trilobite is an extinct group and its age ranges from Cambrian to Permian.
- The body of most of the echinoderms possesses the five-fold or pentameral radial symmetry and has an internal or endo-skeleton.
- Skeleton of a typical echinoid is divisible into the apical system, corona and peristone.
- The geological age range of echinoids is from the Ordovician to the present. Echinoids were a dominant group of invertebrates during the Mesozoic.
- Skeleton of a crinoid consists of three parts: stem, calyx and arms.
- The geological age range of crinoids is from Ordovician period to present. Crinoids were a significant group of invertebrates during the Palaeozoic.

16.8 TERMINAL QUESTIONS

1. Describe with neat sketches the morphological features of a trilobite.
2. Write major morphological characters of echinoids and crinoids.
3. Give a short account of the geological history of trilobites.
4. Discuss the geological history of echinoids and crinoids.

16.9 REFERENCES

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16.10 FURTHER/SUGGESTED READINGS

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- Shah, S.K. (2013) Elements of Palaeontology, Geological Society of India, Bangalore.

16.11 ANSWERS

Self Assessment Questions

1 a) ii)

b) Cephalon or head shield, thorax and pygidium or tail are the transverse divisions of a trilobite skeleton. Longitudinally, the skeleton of a trilobite is divisible into one central axial lobe and two pleural or lateral lobes.

c) Cephalon or head shield is the dorsal part of a trilobite skeleton covering the head. It lies on the anterior margin of the skeleton and is semi-circular in outline. Cephalon is formed by the fusion of five to seven segments. It is made up of glabella and cheeks. The raised axial (central) area of cephalon is known as **glabella**. The portion of cephalon surrounded by the glabella is termed as **cheeks**. Cheeks are further divided into free and fixed cheeks by the facial suture.

d) iii)

e) iii)

2 a) The three characteristic features of echinoderms are:

I. they have a rigid mesodermal skeleton composed of interlocking plates and spines of calcite,

II. their body have five-fold or pentameral radial symmetry, but some advanced forms show bilateral symmetry, and

III. they have a water vascular system.

b) The three parts of a typical echinoid test are: i. apical system or disc, ii. corona and iii. peristome.

c) ocular and genital plates.

d) b).

e) Geological age range of echinoids is from Ordovician to present.

3 a) iii).

b) i).

c) The major hard parts of a crinoid body are: i) stem, ii. calyx and iii. arms.

d) The geological age range of crinoids is from Ordovician to present.

Terminal Questions

1. Refer to the subsection 16.2.2.
2. Refer to the subsections 16.5.2 and 16.6.2.
3. Refer to the subsection 16.2.3.
4. Refer to the subsections 16.5.3 and 16.6.3.

Glossary

Ammonoid : An extinct group of marine cephalopod molluscs belonging to the subclass Ammonidea of the phylum Mollusca. The name Ammonoidea is derived from the Egyptian God “Ammon”. The God “Ammon” is often depicted with ram’s horn behind the ears and the tightly coiled shells of ammonoids resemble ram’s horns, hence they are known as Ammonoidea. They have a coiled shell with complex sutures. They first appeared in early Devonian and became extinct at the end of Cretaceous.

Sea anemone : Belongs to phylum Cnidaria. It is a close relative of corals, which lives on the sea floor with its tentacles pointing upwards.

Aragonite : A mineral form of calcium carbonate ($CaCO_3$), which is commonly found in the shells of many marine organisms.

Arthropods : The name Arthropoda is derived from two Greek words **arthron** meaning joint and **podos** meaning leg, which together referring **jointed leg**. All arthropods have bilateral symmetry, a segmented body along with a hard exo-skeleton.

Apex : Tip or top of the shell.

Beak : A sharp pointed tip of the valve representing the initial growth of the shell and generally lies near or above the hinge line.

Belemnites : Belong to an extinct order Belemnitida of the phylum Mollusca. They existed during the Mesozoic.

Benthos : Marine animals that live on, in, at or near the sea bed.

Bivalves : Belong to the class Bivalvia of the phylum Mollusca. Bivalves are characterised by their two equal and hinged valves.

Brachiopods : Marine animals belonging to the phylum Brachiopoda. They are characterised by having two asymmetrical valves.

Brittle stars : Marine animals belonging to the phylum Echinodermata and closely related to starfish.

Buoyancy : The capacity of a shell to float or to rise in the sea water.

Burrow : A tunnel or hole made into the sediment by an animal to create a space suitable for habitation or temporary refuge.

Calcite : A form of the mineral of calcium carbonate ($CaCO_3$), which is utilised by many organisms to make their skeleton or shells. Calcite and aragonite are both carbonate minerals and have the same chemical composition ($CaCo_3$), but in the two minerals the packing of carbonate ions is different. The chemical structure of calcite is more stable, as a result, shells of invertebrates made up of calcite are chemically stable and do not get dissolved in the same marine conditions under which they are formed and have more chances for their preservation. The structure of aragonite is less stable so, the shells with aragonite composition usually get dissolved under the same marine conditions in which they form, leaving less chance for their preservation.

Calcium carbonate : A chemical compound having chemical formula $CaCO_3$. It is found mainly in sedimentary rocks such as limestone and dolomite, and is also a main component of shells of marine organisms.

Carnivorous : Flesh or meat-eating organisms.

Cephalopods : Marine animals belonging to the class Cephalopoda of the phylum Mollusca. They include animals with chambered shells. The name Cephalopoda is derived from Greek words **Cephalo** meaning head and **Podos** meaning foot, referring to head and foot, which signifies that the foot is directly attached to the head.

Chitin : A hard organic material made up of protein. It forms the exo-skeleton of arthropods and is found in cell walls of fungi.

Chitons : Marine animals belonging to the class Polyplacophora of the phylum Mollusca. The shells of chitons consist of eight hard calcareous plates or valves.

Cirri : A root-like structure of the stemless crinoids.

Cladistics	:	A system to classify organisms based on their evolutionary history in terms of shared and derived characters.
Clams	:	Bivalves that burrow under the sea floor. They belong to the class Bivalvia of the phylum Mollusca.
Commissure	:	The line along which the two valves of bivalves and brachiopods join.
Conch	:	A shell.
Corallum	:	A skeleton of a simple coral.
Corallite	:	A skeleton of each coral polyp in a colony of corals.
Corals	:	Colourful and flower-like simple sea animals belonging to class the Anthozoa of the phylum Cnidaria. They generally have a hard exo-skeleton and mostly live in colonies.
Coral reefs	:	Underwater hard and consolidated structures formed of calcium carbonate secreted by corals.
Cuttlefish	:	Marine animals belonging to the class Cephalopoda of the phylum Mollusca. A cuttlefish possesses an internal structure called the cuttlebone and hence its name. Despite their name, cuttlefish are not fish but true molluscs.
Deep marine/sea floor	:	Includes the continental slope and abyssal plain. The continental slope is the sloping region between a continental shelf and a continental rise, i.e., between 200 m to 5 km. The abyssal plain lies at the depth of 3 to 6 km below the sea level.
Dentition	:	A set of teeth; in molluscs it includes hinge teeth and sockets.
Dextral shell	:	A shell with clockwise coiling and aperture on the right side.
Ecological niche	:	The way in which an organism interacts with its environment and community; it is the status of an organism in its environment.
Endo-skeleton	:	An internal supporting skeleton originating from mesodermal cells found in vertebrates and echinoderms.

Epifaunal	:	Includes those organisms, which live on the top of substratum, not within the sediment.
Exo-skeleton	:	Supporting and protective covering; outside/external skeleton, e.g., found in arthropods and molluscs.
Extinct animals	:	Those species which are no longer living.
Foramen	:	Asmall opening of the shell/bone.
Fossils	:	Remains of past or ancient life commonly preserved in sedimentary rocks.
Gastropods	:	Marine and terrestrial coiled animals belonging to class Gastropoda of the phylum Mollusca. The term Gastropoda is derived from two Greek words, Gastro means stomach (belly) and Pod means foot, (i.e., stomach-foot), which signifies the position of foot on the ventral margin of the animal.
Geological history	:	The story of a changing Earth over billions of years; in an organism's context, it focuses on the origin, evolution, biogeography, and phases of extinction and diversification of life.
Globular	:	The spherical shape.
Growth lines	:	The lines on the surface of a shell marking the position of the margin at some stage of growth.
Heart urchins	:	Burrowing echinoids belonging to the class Echinoidea of the phylum Echinodermata. The body of a heart urchin is usually oval or heart-shaped.
Hinge line	:	An imaginary zone of attachment where two valves of brachiopods or bivalves open and close.
Holdfast	:	A root-like structure occurring at the base of crinoid stems that firmly attaches the animal to the seabed.
Hydrostatic pressure	:	The pressure coming from the weight of the liquid/water.
Imperforate shell	:	A shell with no holes or pores.
Index fossil	:	A fossil that has short geological range and wide geographical distribution e.g., ammonoids. These are used to identify or date geological periods.

Infaunal : Includes animals living within the sediment and not on the top of sediment.

Invertebrates : Animals with no backbone or vertebral column, e.g., molluscs, corals, brachiopods.

Jellyfish : Free-swimming marine animals belonging to the phylum Cnidaria.

Limpets : A group of marine snails belonging to the class Gastropoda of the phylum Mollusca. They have a simple and broadly conical shell.

Living chamber : The last developed chamber of a cephalopod shell where the animal sits.

Living fossil : An organism or species which has retained its original morphological characters over millions of years, has no living relatives and represents a sole survivor of the group. Some examples include the cephalopod *Nautilus,* the brachiopod *Lingula* and the plant *Ginkgo.*

Lophophore : A feeding and respiratory organ found in brachiopods.

Marine : Pertaining to the oceans.

Marine animals : Include all animals that live in the ocean

Mollusca : A diverse group of animals belonging to the phylum Mollusca of the kingdom Animalia. Gastropods, bivalves and cephalopods are its main representatives. The name Mollusca is derived from the Latin word **molluscus** and refers to the soft-bodied animal enclosed in a shell.

Morphology : Study of the forms and structure of organisms.

Mussels : Marine to fresh water animals belonging to the class Bivalvia of the phylum Mollusca and their shells are elongated and asymmetrical in outline**.**

Nautiluses : Marine animals belonging to the class Cephalopoda of the phylum Mollusca. They have an external coiled shell. Nautiluses include living genus *Nautilus.*

Nekton : A swimming animal that live in an open ocean.

Nocturnal : Includes those animals that are active in night.

Nudibranchs	:	Sea snails having no shell and belong to the Phylum Mollusca.
Ocean bottom	:	The bottom of a sea or ocean.
Ocean floor	:	A part of the Earth's surface beneath the seas and the oceans.
Octopuses	:	Cephalopod molluscs which belong to the order Octopoda. They have two eyes and four pairs of arms with bilateral symmetry and no internal or external skeleton.
Oysters	:	Marine bivalves belonging to the class Bivalvia and the phylum Mollusca.
Palaeontologist	:	A scientist who studies fossils.
Palp	:	is an elongated appendage which is found usually near the mouth of molluscs and its functions include sensation, locomotion and feeding.
Parasite	:	An organism that lives on or in a host (another organism) and gets its food from the host. Equivalent
Pedicle valve	:	The valve in a brachiopod shell that contains the pedicle.
Pelagic life	:	is the life of pelagic zone.
Pelagic zone	:	The area of the ocean outside of coastal areas and it contains some of the biggest marine animals.
Pentameral symmetry	:	A five-fold symmetry, a characteristic feature of echinoderms.
Perforate shell	:	A shell with holes or pores.
Periwinkles	:	Small marine snails belonging to the class Gastropoda of the phylum Mollusca.
Phragmocone	:	A chambered part of a cephalopod shell.
Planispiral coiling	:	The coiling of the shell in one direction.
Plankton	:	An organism that floats in the ocean or in lake waters.
Polyp	:	A single coral animal.

Predator	:	An animal that preys on others.
Protoconch	:	The first or original shell.
Rudist bivalves	:	An extinct group of box, tube or ring shaped marine bivalves. They had two asymmetrical valves with one valve attached to the sea floor. First appeared during the Jurassic and became extinct at the end of Cretaceous. Their fossils are found in the tropics in the Mediterranean, the Middle East, Caribbean and Southeast Asia.
Sand dollars	:	Burrowing sea urchins belonging to the class Echinoidea of the phylum Echinodermata.
Scavenging	:	Feeding on dead organisms
Scallops	:	Marine bivalves.
Sea bed	:	The bottom of the ocean and is also known as the seafloor, sea floor, or ocean floor.
Sea anemone	:	A close relative of corals, which lives on the sea floor with tentacles pointing upwards.
Sea cucumbers	:	Marine animals with a leathery skin and elongated body. They belong to the class Holothuroidea of the phylum Echinodermata.
Sea fans	:	Marine animals belonging to the class Anthozoa of the phylum Cnidaria.
Sea lilies	:	Plant likes marine animals belonging to the class Crinoidea of the phylum Echinodermata.
Sea pens	:	Colonial marine animals belonging to the class Anthozoa of the phylum Cnidaria.
Sea urchins	:	Small, spiny and globular marine animals belonging to the class Echinoidea of the Echinodermata.
Sessile	:	Animals that live on the ocean floor and which do not move.
Star-fishes	:	Marine animals belonging to the class Asteroidea of the phylum Echinodermata. They grasp their prey with their tube feet.

Shell	:	A hard rigid mainly calcareous covering of an animal.
Shell microstructure	:	Microscopic structure of the shell.
Shipworm	:	A group of unusual marine wood-boring clams belonging to the class Bivalvia of the phylum Mollusca. They have long, soft and naked bodies.
Sinistral	:	A shell with anti-clockwise coiling and aperture on the left side.
Slugs	:	Shell-less land gastropods, which belong to the class Gastropoda of the phylum Mollusca.
Snails	:	The land gastropods. They have a coiled and conical-shaped shell.
Squids	:	Cephalopods, belonging to the class Cephalopoda of the phylum Mollusca. They have a distinct head, a mantle, eight arms and two long tentacles. They are good swimmers.
Systematics	:	The study of biological diversity and its evolution.
Substratum	:	A layer of sediments that lies beneath another layer of sediment.
Surface sculpture	:	The external ornamentation of the shells.
Tentacles	:	Flexible, mobile and elongated organs soft parts present in some invertebrates, e.g., corals, cephalopods. Animals used tentacles mainly for grasping and feeding.
Tooth shells	:	Burrowing marine molluscs belonging to the class Scaphopoda of the phylum Mollusca. They have a long, tapering and slightly curved tubular shell.
Tubercles	:	Small root like extensions from a shell or skeleton.
Umbo	:	The region of maximum curvature of the valve close to the beak.
Univalves	:	Animals with single valves, e.g., gastropods.
Valve	:	One half of a brachiopod or bivalve shell. Two valves together make a complete shell.

Whelk	:	A marine snail.
Wood-boring bivalves	:	Include two groups of bivalves such as shipworms (family Teredinidae) and giant clams (family Tridacnidae) which bore wood as a food source.

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Dear Learner,

While studying the theory course BGYCT-137 (Stratigraphy and Palaeontology), you may have found certain portions of the text difficult to comprehend. We wish to know your difficulties and suggestions, in order to improve the course. Therefore, we request you to please fill out and send us the following questionnaire, which pertains to this course (i.e., BGYCT-137). If you find the space provided is insufficient, kindly use a separate sheet.

Please mail to:
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Discipline of Geology
School of Sciences
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New Delhi – 110068 (India)

Questionnaire

1. Name: ____

2. Enrolment No.

3. Regional centre code and name: ____

4. Study centre code and name: ____

5. How many hours did you spend for studying the each unit?

Course	**BGYCT-137: Stratigraphy and Palaeontology**															
Unit no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
No. of hours																

6. Please give your reactions (by '√' mark) to the following items based on your reading of the theory course:

Items	Excellent	Very Good	Good	Poor	Give specific examples, if poor
Presentation Quality					
Language and Style					
Illustrations used (Diagrams, Tables etc.)					
Conceptual Clarity					
Self Assessment Questions (SAQ)					
Feedback to SAQ					

7. Your specific comments on the course BGYCT:137

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