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.

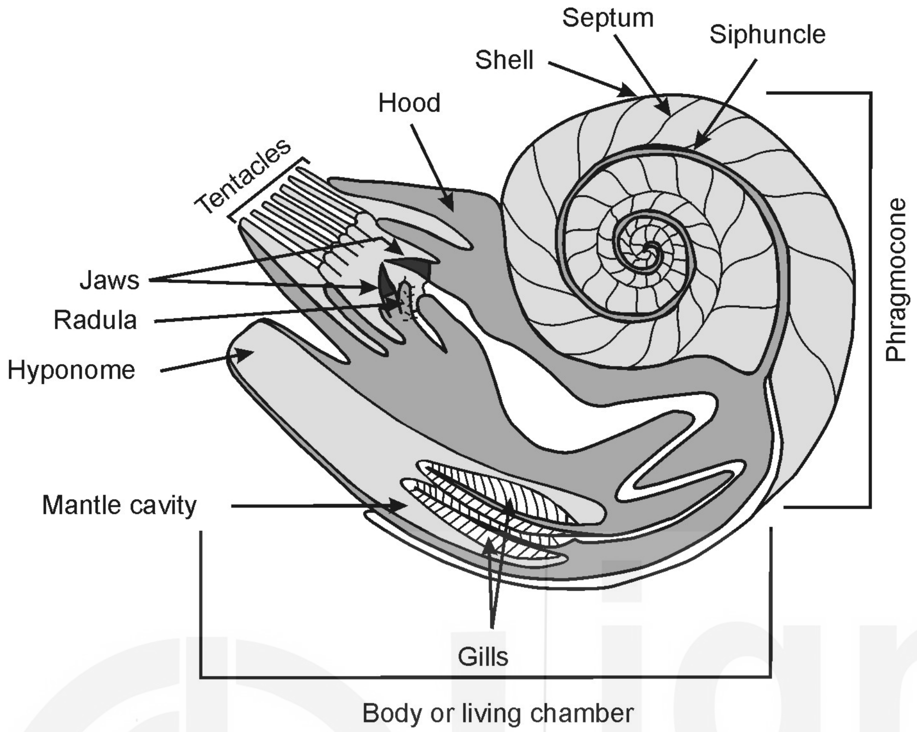

Fig. 15.1: Schematic diagram of living *Nautilus* showing main morphological features. (Source: simplified from Clarkson, 2007; Milsom and Rigby, 2010)

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.

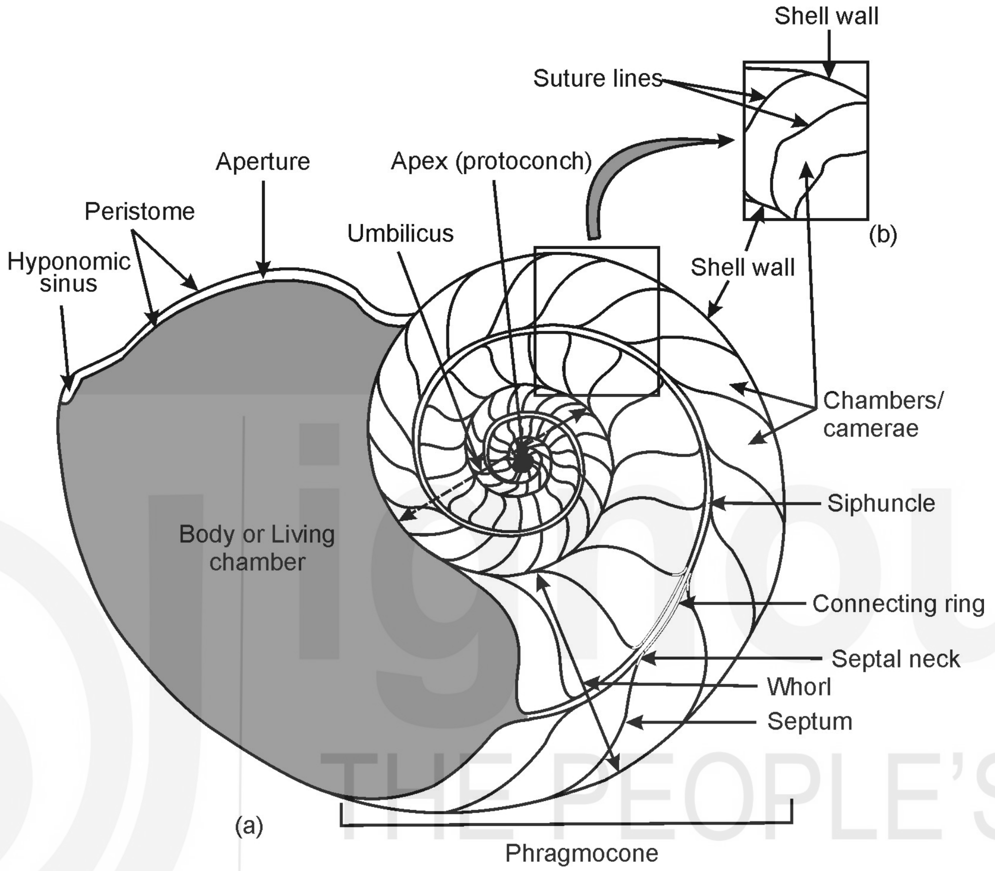

Fig. 15.3: Shell of a nautiloid: a) showing internal morphology; and b) enlarged part showing the suture lines.

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).

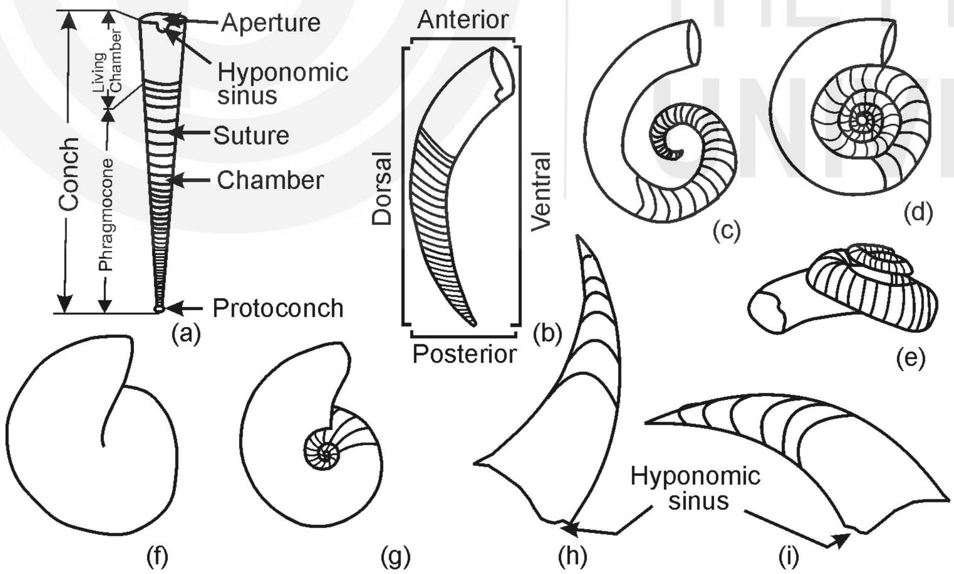

Fig. 15.4: Shells of a nautiloids showing various shell forms: a) Orthoceracone with main shell features; b) Cytoceracone showing the ventral, dorsal, anterior and posterior margins; c) Gyroceracone; d) Traphyceracone; e) Trochoceracone; f) Involute nautilicone; g) Evolute nautilicone; h) Exogastric; 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.

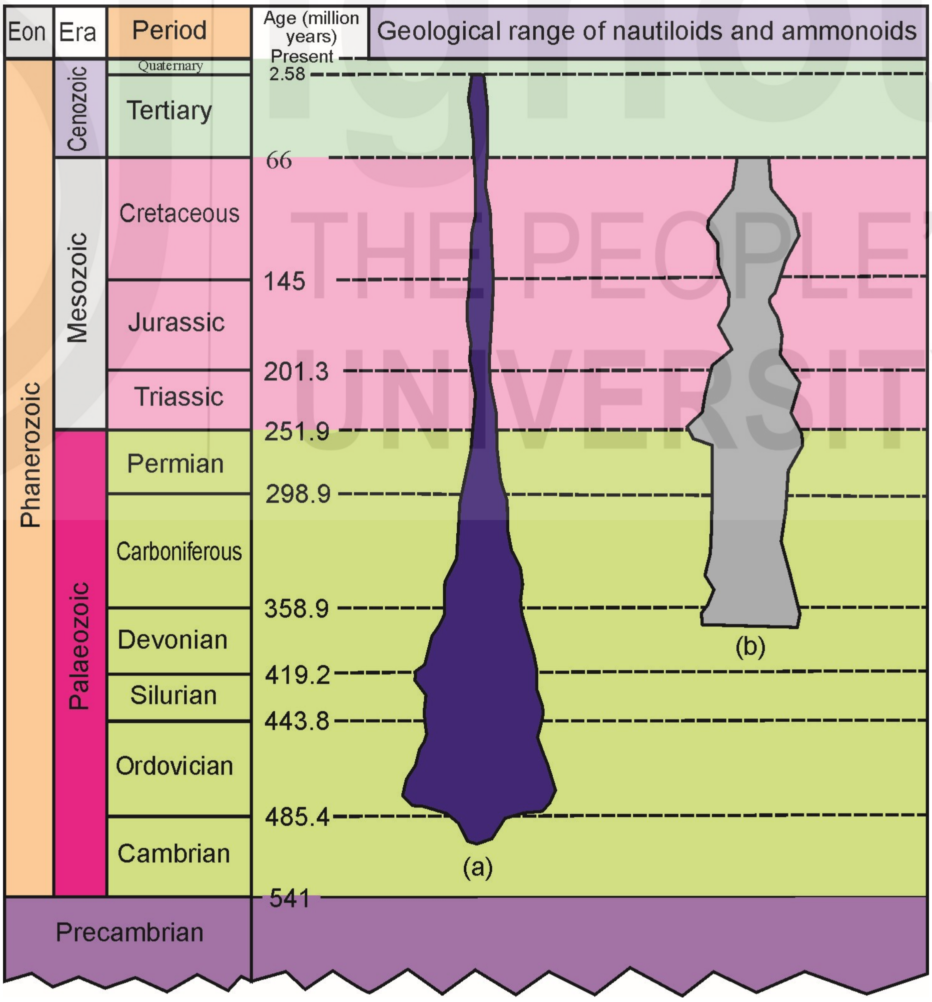

Fig. 15.5: Stratigraphic distribution of cephalopods: a) Nautiloids; and b) Ammonoids. (Source: modified after, Milson and Rigby, 2010)**. Width of column represents the abundance of nautiloids and ammoniods in a particular period/era.**

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**.

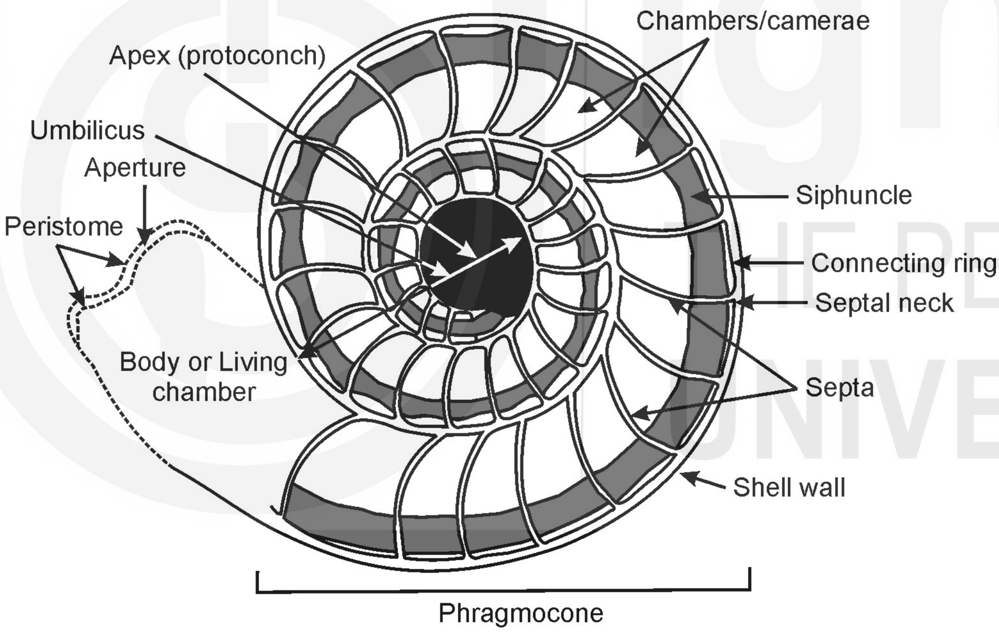

Fig. 15.7: Shell of an ammonoid showing morphological features (Source: simplified after Wood, 2004.

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:

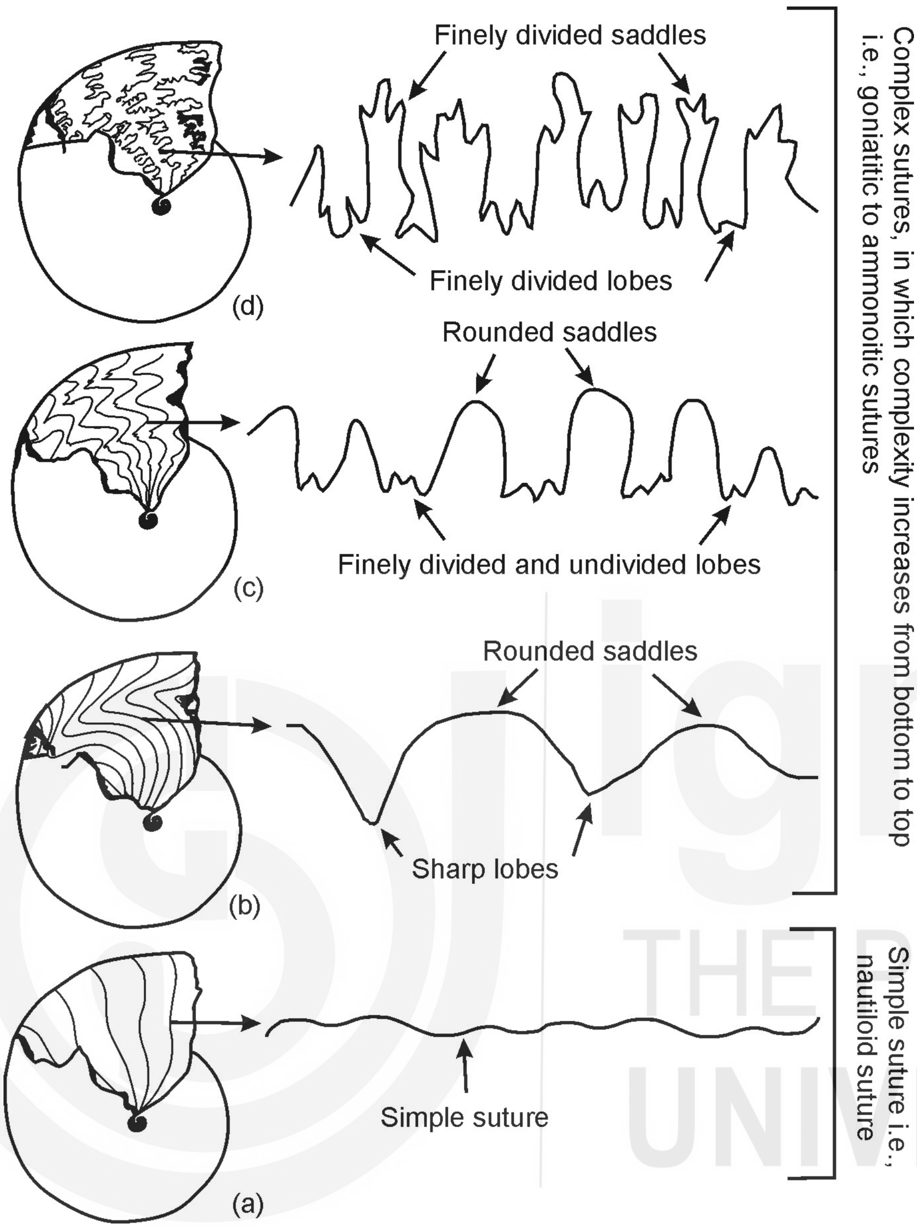

Fig. 11.8: Suture patterns in nautiloid and ammonoid cepahlopods: a) Simple suture line also known as nautiloid suture (b-d) are complex sutures, which are commonly present in ammonoids; b) Goniatitic suture; c) Ceratitic suture; and d) Ammonitic suture. (Source: Shrock and Twenhofel, 1987; Benton, and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

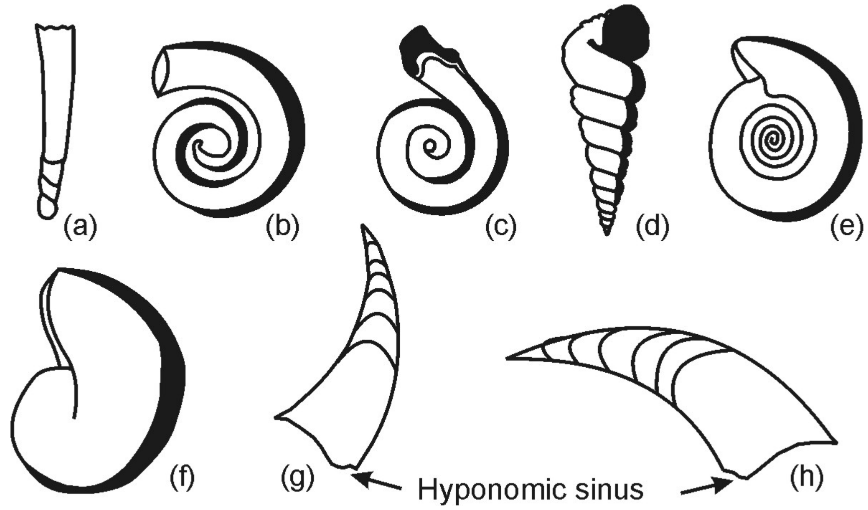

Fig. 15.9: Shells of ammonoids showing various shell forms: a) Bactriticone; b) Gyroceratiticone; c) Dactylioceracone; d) Turriliticone; e) Involute ammoniticone; f) Evolute ammoniticone; g) Exogastric; and h) Endogastric shell forms. (Source: redrawn after Shrock and Twenhofel, 1987)

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.