Invertebrate Macrofossils

Practical 5

Cephalopods – Class Cephalopoda

What are Cephalopods?

- Highly advanced marine molluscs, shallow to deep water
- Cephalo = head, Pode = leg (head bearing tentacles (legs))
- Cephalopods unlike other molluscs have a well developed head brain and elaborate sensory organs with good eyes (functionally parallel with the eyes of the vertebrates)
- The head is surrounded by 8, 10 or more arms or tentacles
- The rest of the body is based upon the basic plan of the bivalves
- Their chambered univalved shell provided the means of effective buoyancy, hence nektonic (swimming) animals
- Exploited the rich food resources of the nektic habitat

- Predatory carnivores
- Among the invertebrates the most accomplished swimmers
- They posses either an external shell or an internal modified shell structure, or the the shell is absent (as in octopus)
- The shell is basically a cone which may be straight, curved or planispirally coiled
- The class includes the modern *Nautilus*, the argonauts, squids, octopuses and cuttlefishes, and the extinct ammonoids and belemnites
- They have an extensive record from the Late Cambrian onwards

Classificaton of cephalopods

- The three subclasses are:

1. Subclass NAUTILOIDEA (U.Camb. - Rec.), external shell (straight, curved or coiled), chambered, simple sutures, central siphuncle, 4 gills
2. Subclass AMMONOIDEA (L.Dev. - end Cret.), external shell (straight, curved or coiled), chambered, complex sutures, ventral or nearly dorsal siphuncle
3. Subclass COLEOIDEA (L.Dev. - Rec.), internal shell (straight or coiled), chambered, siphuncle may be absent, 2 gills

Subclass NAUTILOIDEA

- The nautiloid shell is divided into chambers by saucer-like septa (sing. septum)
- Each septum has an approximately central perforation for the siphuncle, which is surrounded on the posterior convex side of the septum by the septal neck
- The animal lives in the last formed chamber, the body chamber, at the anterior of the shell
- The body is retracted in the aperture and the aperture is closed by a muscular hood
- Only one living representative: the tropical genus *Nautilus,* with six living species

Soft part morphology (based on *Nautilus*)

- Soft parts are separated into:

a. the head-foot

b. the body

The head-foot

- Distinct head with two highly developed, lateral eyes and a mouth
- Around mouth, 38 retractable tentacles without hooks or suckers
- Inside mouth two horny jaws made of chitin with calcified tips, and between them a radula with transverse rows of teeth aiding in food swallowing
- Dorsally, above tentacles a hood with an external tough skin; when head and tentacles are withdrawn and the hood closes the aperture

The body

- Consists of the viscera and the mantle cavity
- The visceral mass is covered by a thin mantle which secretes the shell
- Ventrally, it encloses the mantle cavity which contains two pairs of gills
- The mantle is prolonged as a fleshy cord in a tubular sheath (the siphuncle); it connects all the chambers up to the protoconch (the initially secreted shell) at the apex and controls buoyancy by filling and emptying the chambers and carries blood
- Bellow the tentacles the funnel (or hyponome) is found, a long, flexible tubular structure which leads to the mantle cavity; it brings water to the mantle cavity and gills with gentle and regular movements
- However, when water is ejected with force it propels the animal backwards; by bending the funnel it can change course

The shell

- The shell is made of aragonite in a conchiolin matrix
- It consists of two main layers:

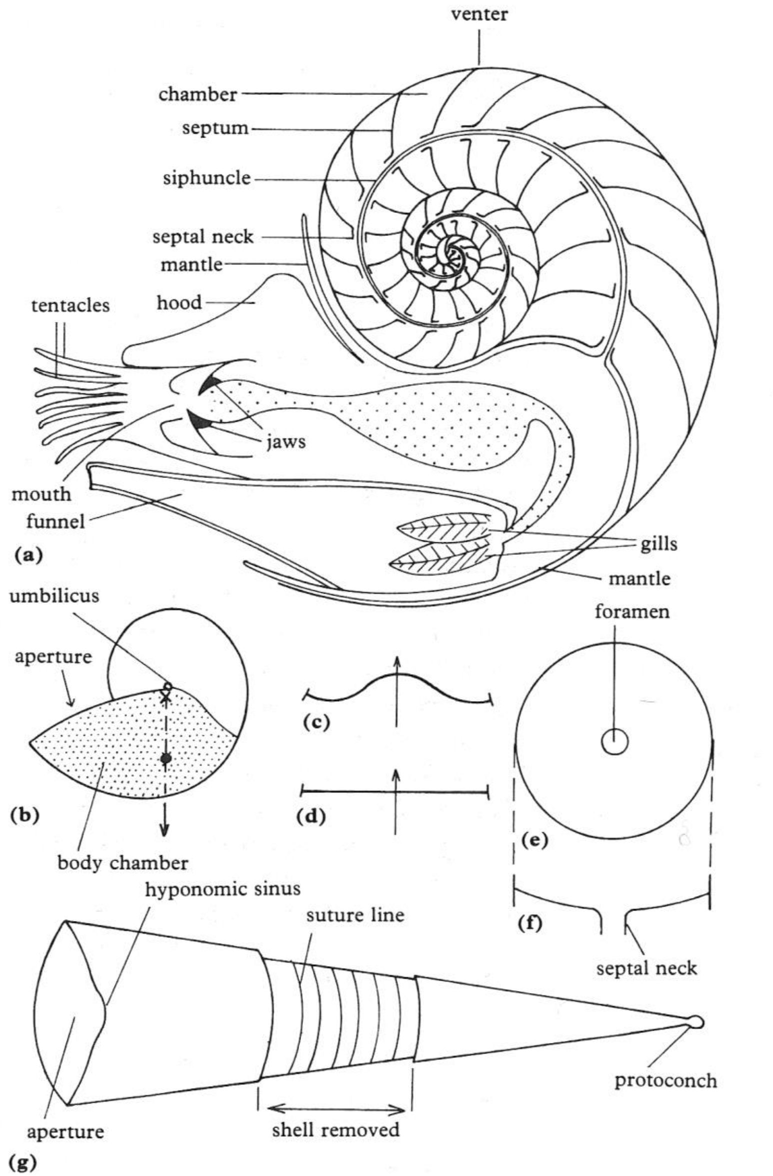
a. A porcellaneous outer layer; it is formed first and is made of aragonite grains in conchiolin that grow into vertical prisms
b. An inner nacreous layer; a brick wall structure of hexagonal aragonite crystals with conchiolin layers between them

The shell

- The simplest form is basically a cone, closed at the apical end (apex) and open at the other end (aperture), the orthocone
- Generally, the shell is curved or coiled planispirally
- The ventral side, the venter, forms the circumference
- The shell (and body) is bilaterally symmetrical
- Successive whorls (complete coils) come in contact
- As the shell widens, the last whorl forms a depression on each side, the umbilicus
- A loosely coiled shell is an evolute shell; it possesses a wide umbilicus
- A tightly coiled shell is an involute shell; the umbilicus is small as each whorl embraces the previous one

The shell

- The chambered part of the shell is called phragmocone
- The septa of the chambers are concave forwards
- The septal edges form lines, the suture lines
- They are straight in orthocones, gently undulating in coiled shells
- The central perforation in septa, is called foramen, septal neck at the posterior side (towards the apex)
- The last chamber is relatively large (1/3 of the last whorl)
- The shape of the aperture may be round or oval
- An embayment at the ventral side of the aperture, the hyponomic sinus, to accommodate the funnel



42 Morphology of the nautiloids.

a–c, *Nautilus*: a, a simplified median section of the shell to show the arrangement of the soft parts and internal structures; b, attitude of the shell when floating in water (the cross marks the approximate position of the centre of buoyancy, and the filled dot the centre of gravity); c, suture line (the arrow is pointing in the direction of the aperture). d–g, *Orthoceras*: d, suture line; e, anterior view of a septum; f, transverse section of a septum; g, idealised view of a shell showing the main features.

Representatives

- The modern *Nautilus*

  large up to 30cm, with an involute shell and simple sutures, a nektonic predator.
- The *Orthoceras* (L. Ordovician – L. Triassic)

  Orthocone, with cylindrical adult part, circular cross section, suture straight, hyponomic sinus, may reach several meters in length

‘*Nautilus*’ *imperialis*, London Clay, Eocene (× 1).

Subclass AMMONOIDEA

- Coiled, usually planispiral shell
- Complex folded septal partitions and sutures lines
- Forward pointing septal necks in the adult shell (towards the aperture)
- Slender siphuncle close to the ventral margin
- Ovate embryonic shell (protoconch)
- *Nautilus*, point of reference as it possesses external chambered shell, however marked differences between the two shells (probably, the same for the soft body)

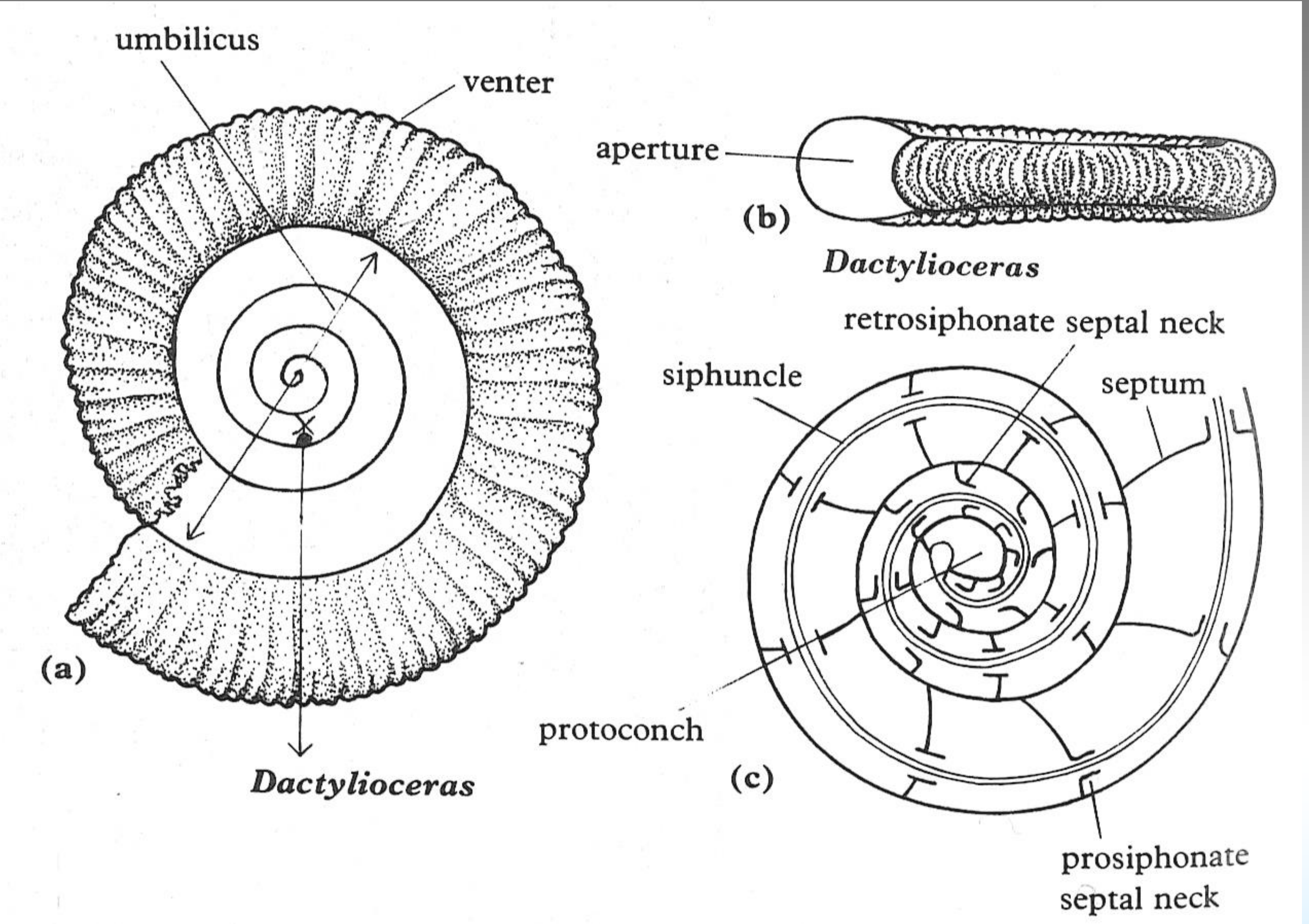
The shell

- Consists of three parts:

1. The protoconch (embryonic shell)
2. The phragmocone
3. The body chamber

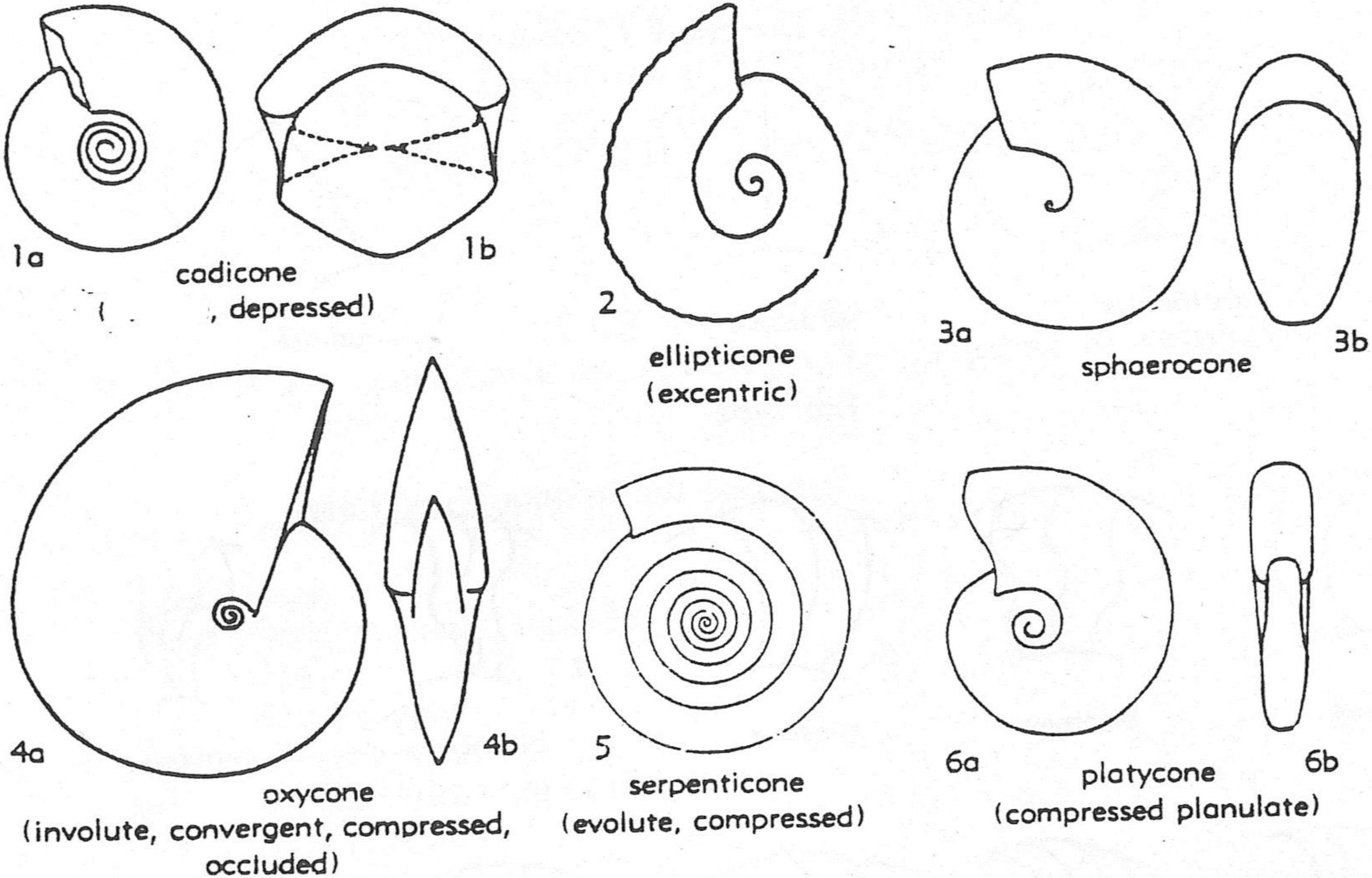
The shell

- It is made of aragonite
- Similar to that of *Nautilus* but thinner
- In most ammonites planispirally coiled
- However, it may be straight, curved, combined initial coiling with a distal straight or hooked section or in exceptional cases helicoid spiral
- The size ranges from 1 cm to 3 m


umbilicus
venter
aperture
(b)
Dactylioceras
retrosiphonate septal neck
siphuncle
septum
(a)
protoconch
(c)
Dactylioceras
prosiphonate
septal neck

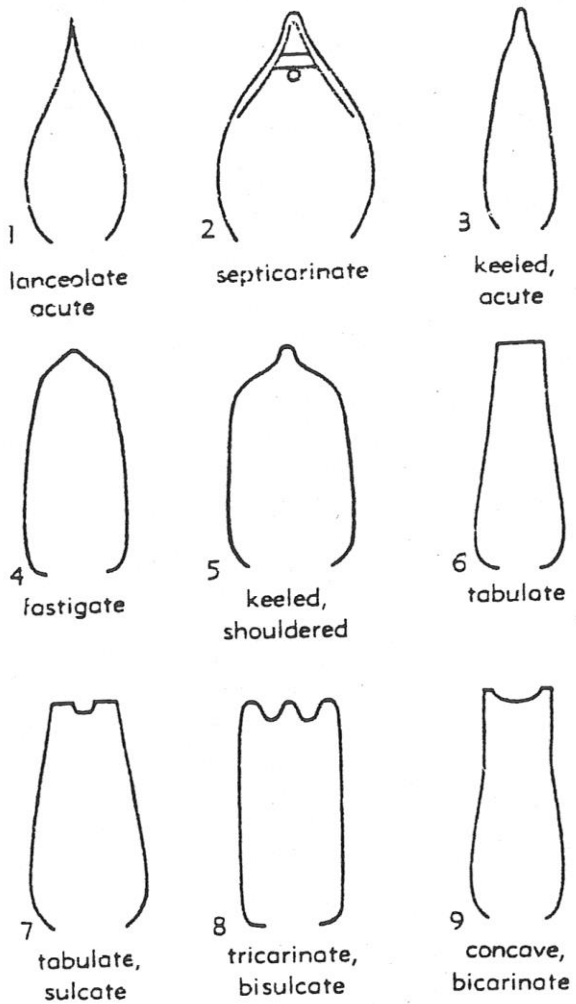
Planispiral shells

- When loosely coiled: evolute
- When tightly coiled: involute
- According to the shape/form of the cross-section or whorl section: round, oval, quadrate, compressed, triangular or depressed
- According to the degree of coiling and shape of whorl section: cadicone, ellipticone, sphaerocone, oxycone, serpenticone, platycone

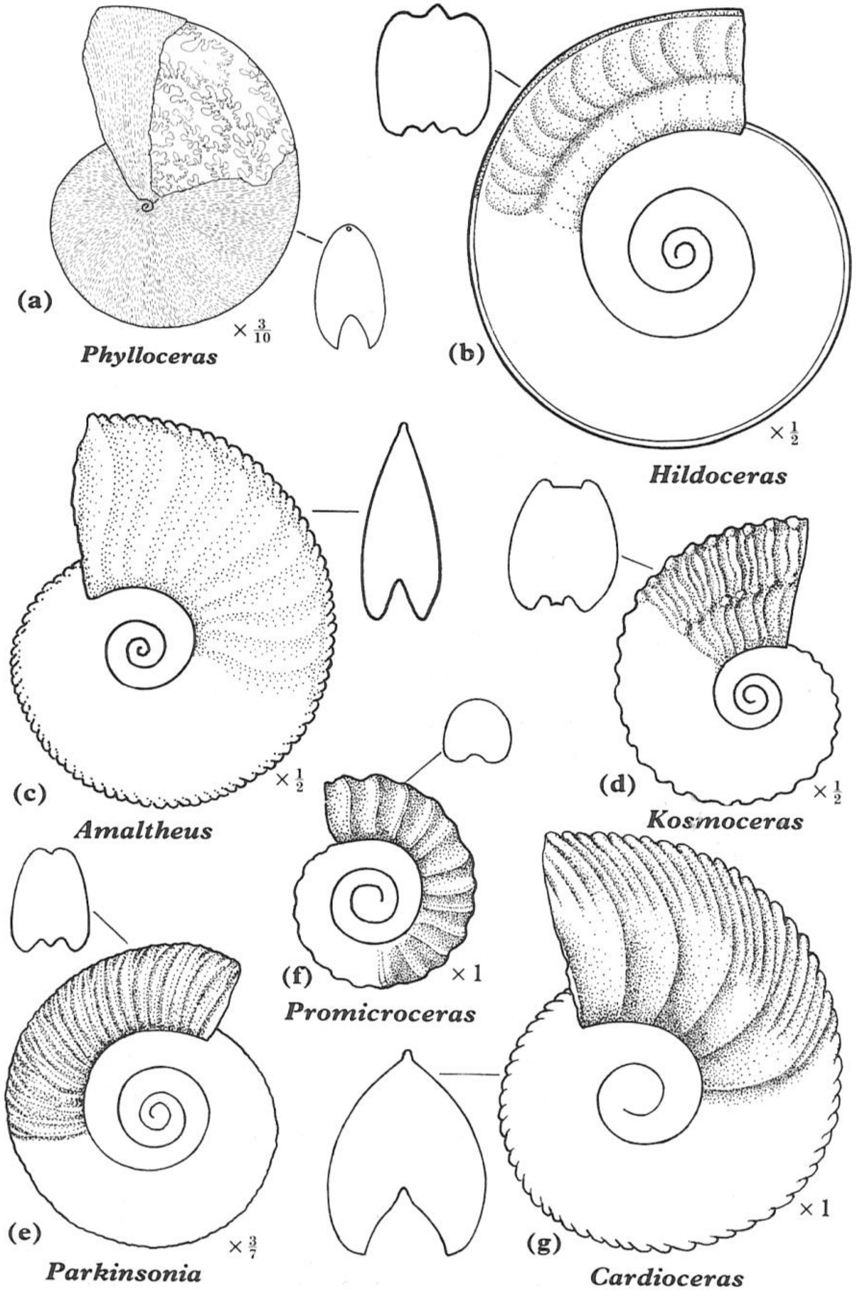


Types of coiling in ammonoid conchs; planispiral forms

Whorl section



Types of whorl sections and venters of ammonoid conchs



55 **Jurassic ammonites.**

Suture lines

- As in nautiloids the phragmocone is divided into chambers by septa
- However, the suture lines are much more complex, folded structures
- the forward (towards the aperture) pointing folds are called saddles and the backward folds (towards the apex) are called lobes
- The folding is shallow in primitive ammonoids and in the early septa of individuals, but it may be intensely crimped in the adults of the advanced ammonoids
- a feature, developed, perhaps, to withstand pressure in deep water

Suture line patterns

1. goniatitic suture: both lobes and saddles are entire; typical of the goniatitids (Palaeozoic)
2. ceratitic suture: the saddles are entire but the lobes are toothed; typical of the ceratitids (Permian and Trias)
3. ammonitic or phyloceratitic suture: both lobes and saddles arc intricately frilled; typical of the ammoniticls (Permian and Mesozoic)

- In diagrams only one part is drawn; starting from the venter (this is indicated by an arrow pointing towards the aperture), and ending at the margin of the umbilicus

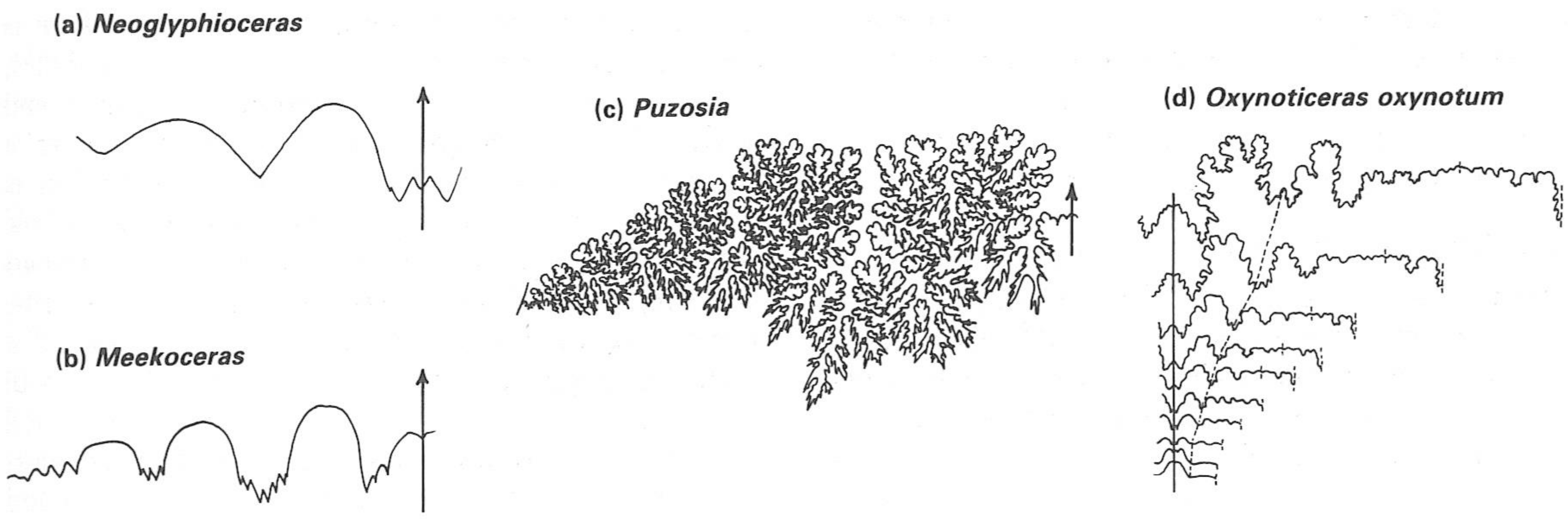
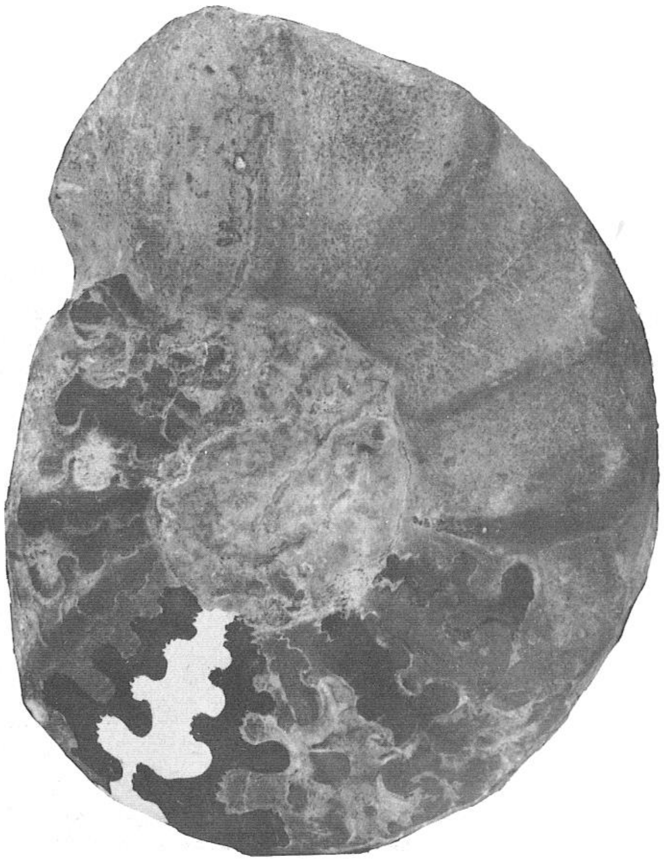


Figure 8.24 Suture morphology in ammonoids: (a) goniatitic suture (*Neoglypheoceras*) (L. Carb.); (b) ceratitic suture (*Meekoceras*) (Trias); (c) ammonitic suture in *Puzosia* (L. Cret); (d) sutural ontogeny in *Oxynoticeras oxynotum* (Jur.). (Modified from various authors in *Treatise on Invertebrate Palaeontology*, Part L)

58 **Triassic ammonite showing ceratitic suture:** ***Ceratites*****, M Trias** (× 1.3).

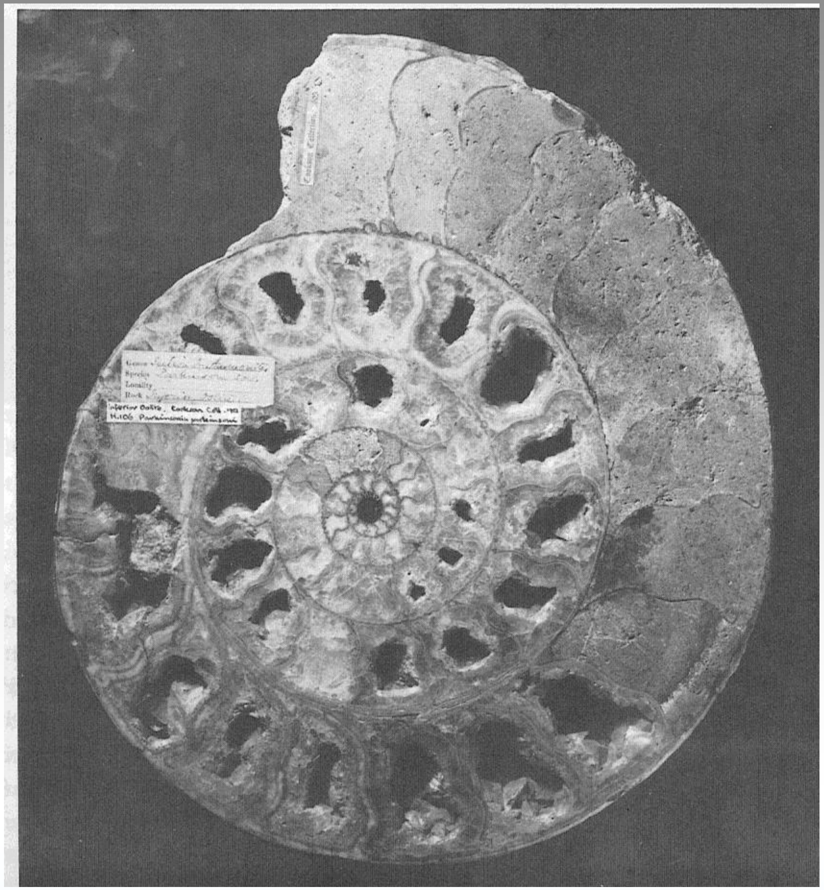


Phylloceras

- The siphuncle in most ammonoids shifts outwards and lies on the margin immediately under the venter in later whorls (in the Devonian clymeniids, however, it lies on the dorsal, inner margin)
- Short septal necks encircle the siphuncle where it passes through the septa
- the septal necks project towards the aperture (prosiphonate) in the later-formed septa of Mesozoic ammonitids but in the earliest ammonoids (as also in the nautiloids) they project towards the apex (retrosiphonate)

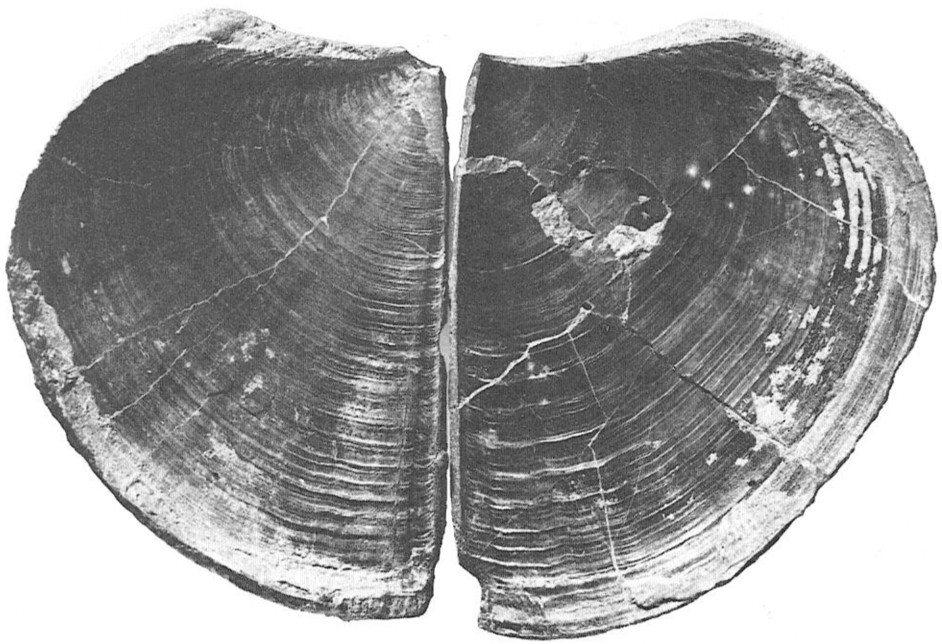
50 The siphuncle seen at a, and septal necks at b, in part of the section shown in fig. 49 (× 1).

- The body chamber varies in length; it may occupy only half a whorl in stout shells, or more than one whorl (360°) in slender shells
- It is not always preserved; it lacks the support afforded the phragmocone by the septa and was, perhaps, the more easily broken
- The aperture is, in general, of similar shape to the whorl section
- in some forms it is constricted or modified by projections of shell. Lateral projections (one on each side) are lappets, and a ventral projection is a rostrum


Genus
Species
Locality
Rock

Anaptychus - aptychi

- Where the body chamber is well preserved, parts of the jaws may be found inside it
- The lower jaw in some forms is a horny plate made of conchiolin the anaptychus
- in other forms it consists of a pair of calcite plates, the aptychi, lying side by side (calcareous thickening of the anaptychus)

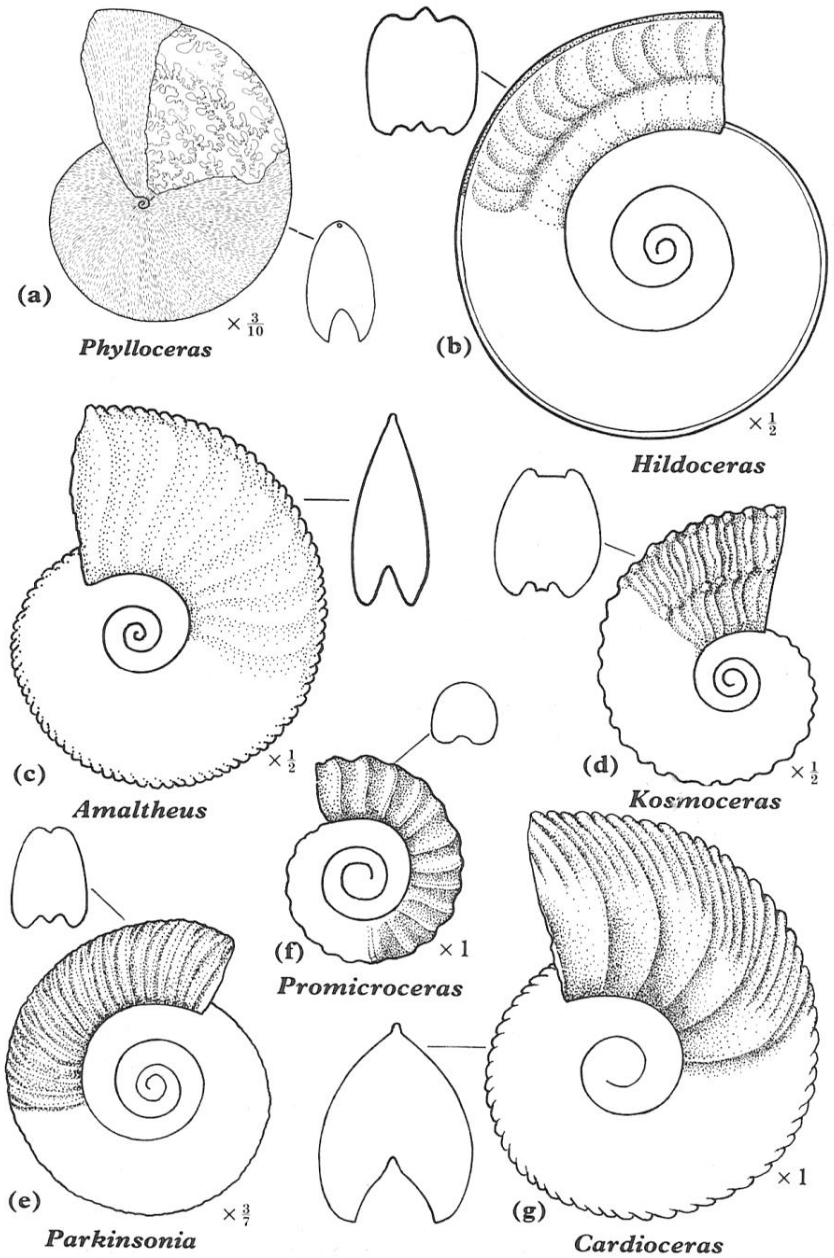


51 Aptychi, Kimmeridge Clay, U Jurassic (× 1.5).

- usually separated from the shell on death and are well known as discrete and flattened fossils
- In life the lower jaw lies in the body chamber, towards the aperture, associated with a smaller upper horny jaw and, in some cases, with the remains of the radula lying between them (form jaws comparable with those of the octopus)
- The two aptychi may, where the fit in the aperture is good, have had a secondary function as an operculum or lid, an interpretation extended in the past to all these plates
- Jaws have been found in a variety of ammonoids, anaptychi from Devonian to Cretaceous; aptychi appearing in the lower Jurassic. Jurassic and Cretaceous may be more specialised, the lower jaw forming a longer scoop-like structure. The diversity now known suggests differences in feeding strategies

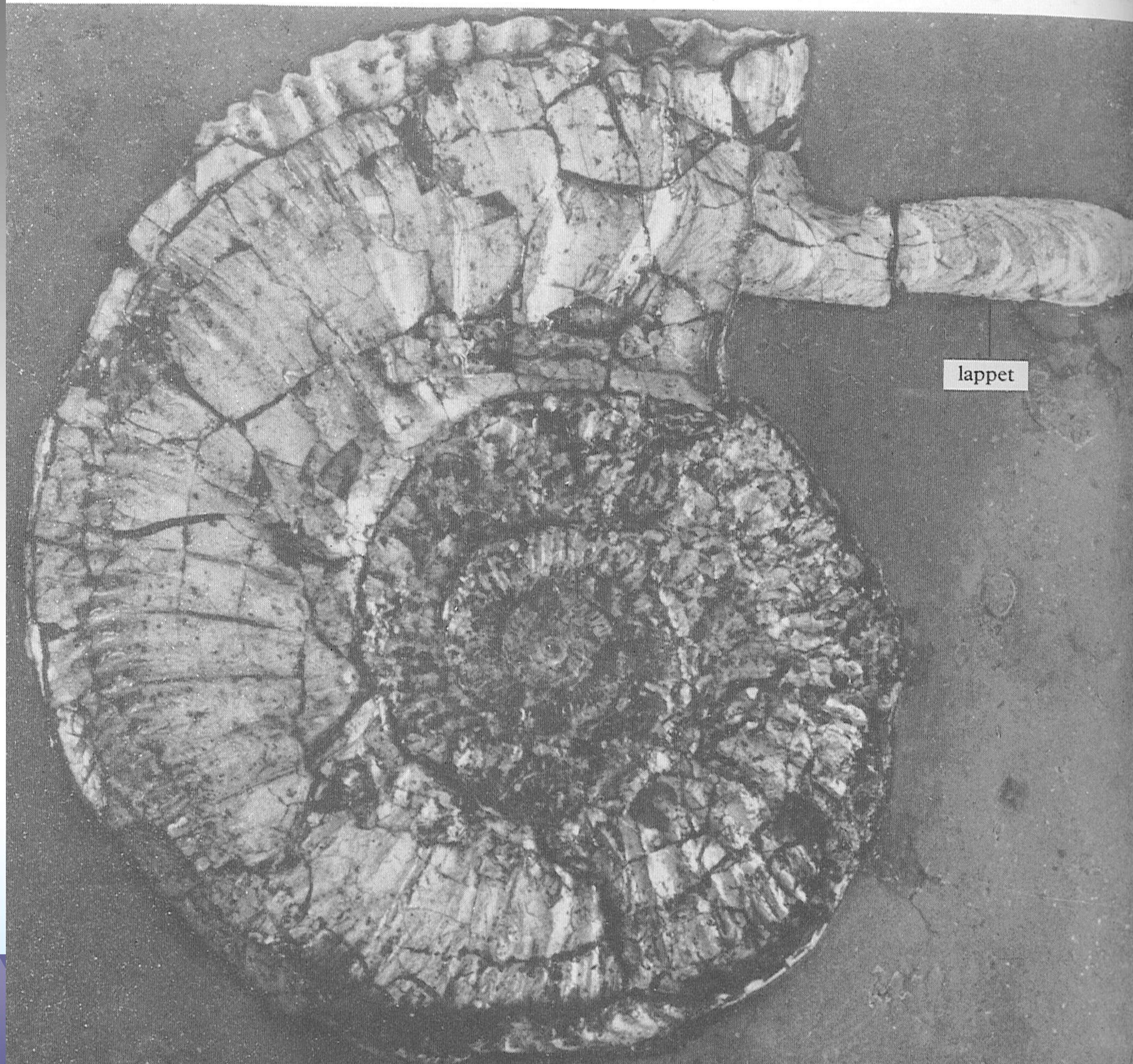
Ornament

- The shell may be smooth
- It may be ornamented by fine lines (striae), ribs, tubercles or spines (especially in Mesozoic forms)
- Ornament may be transverse, spiral or both
- It may be confined to the sides, or may also occur on the venter
- Some forms may have a groove (sulcus) on the venter, or a ridge (keel)
- The ornament may be a localised thickening, but more generally it is a folding of the shell



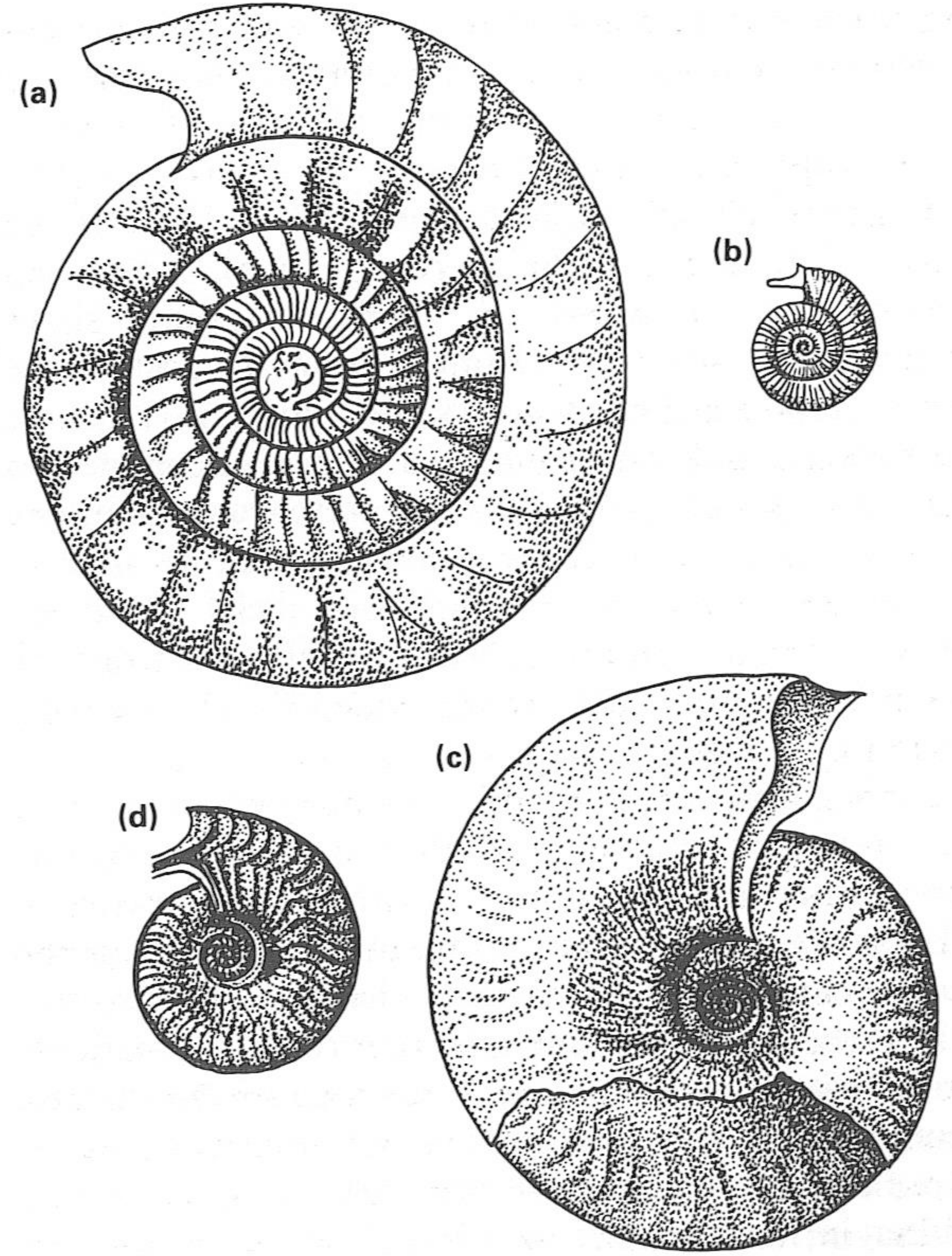
55 Jurassic ammonites.

59 **Jurassic ammonite with lappet: *Kosmoceras*, Oxford Clay, U Jurassic (× 1.7).**



Dimorphism

- The sexes are separate and may be unlike in living cephalopods
- mature shells of certain ammonite species which occur in paired groups in the same bed
- one of the pair is large, macroconch, the other is small, microconch
- If this view is correct, such pairs actually represent a single species with distinct dimorphism
- The macroconch is interpreted as the female (the extra space was needed to contain eggs, and also by analogy with living coleoid cephalopoda)
- In some cases lappets distinguish the aperture of the microconch



(a)
(b)
(c)
(d)

Heteromorps

- some groups of ammonites evolved shells of highly aberrant form and are known as heteromorphs
- Some appeared during the late Triassic, some in the Jurassic, but more extensive development of heteromorphs during the later Cretaceous
- The shell loosely coiled with the whorls wholly or partially separated, other genera are almost straight, others have the body chamber hooked over the top like a walking stick and other genera, are helically coiled like gastropods

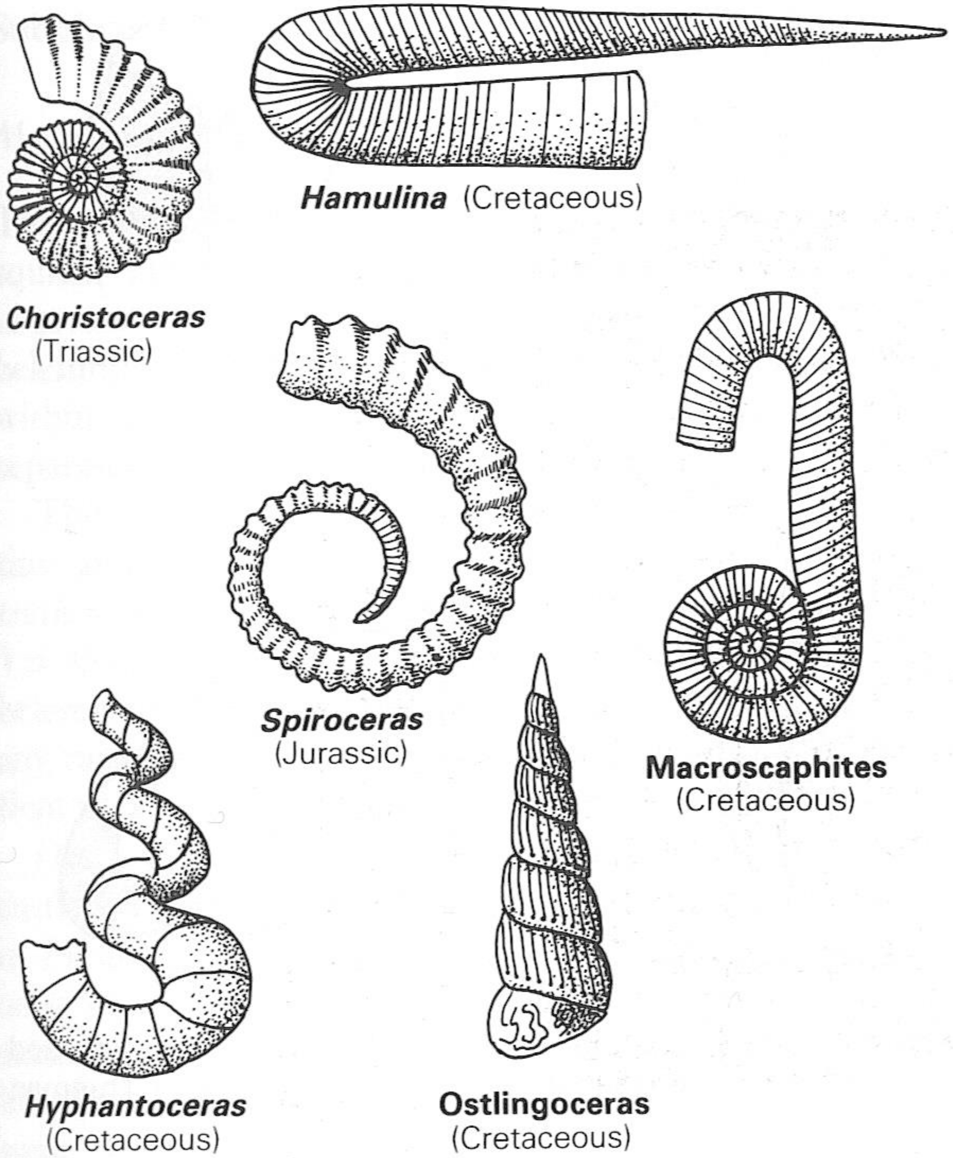


Figure 8.28 Heteromorphic ammonoids, showing variety in form. (Redrawn from *Treatise on Invertebrate Paleontology*, Part L)

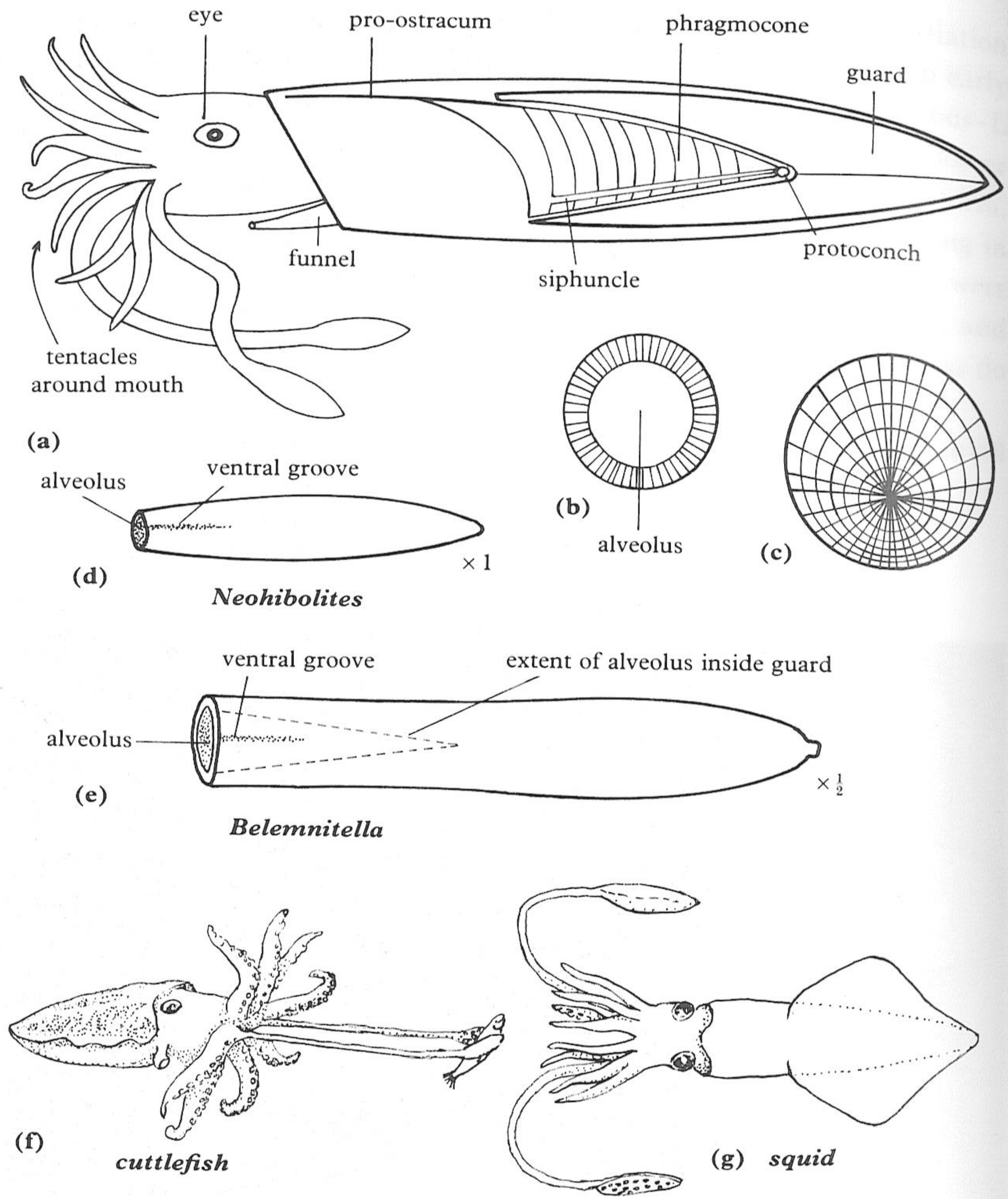
Subclass COLEOIDEA

- the coleoid shell is internal and, in living forms, is modified or rudimentary
- The fossil record of living forms, i.e. squids (Teuthida), cuttlefish (Sepiida) and octopuses (Octopodida) is meagre
- Belemnites, however, with more substantial shell, are common fossils especially in the Jurassic and Cretaceous

The belemnite shell

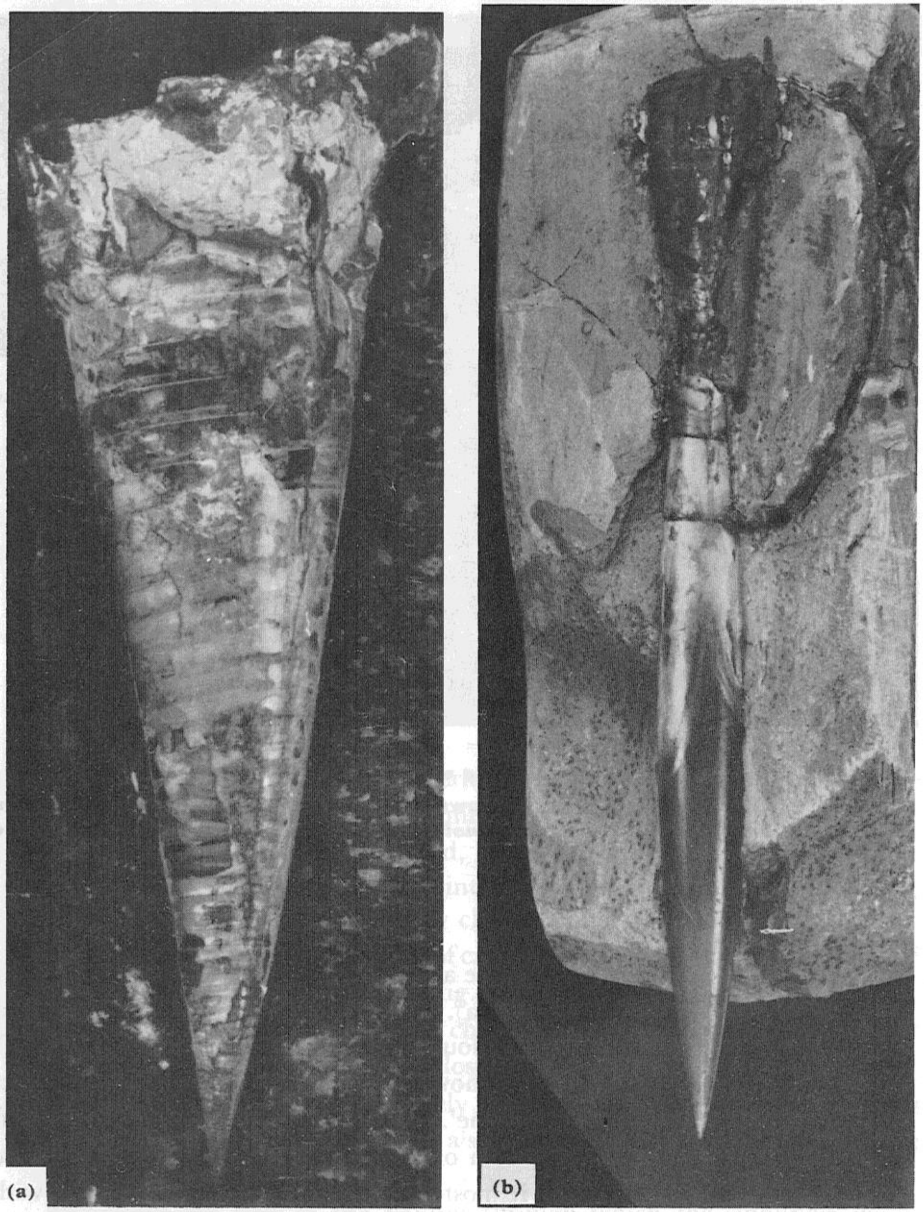
- The belemnite skeleton consists of a phragmocone which was partly contained in a cavity in one end of a solid calcitic guard
- The guard is normally the only part preserved of the belemnite shell.
- It is a cigar-shaped solid structure, tapered at the posterior end, and with a deep conical cavity, the alveolus, at its anterior end
- In most genera the guard ranges 2-20 cm in length.
- In transverse section the guard shows a fibrous structure with tiny calcitc prisms radiating from an eccentric point; rings concentric about this point denote growth stages.
- The phragmocone is a conical chambered shell with thin delicate walls and is less commonly preserved
- The posterior end, with the oval protoconch at its tip, lies within the alveolus of the guard

- There is no body chamber
- the anterior end is drawn out dorsally as a fragile horny process, the pro-ostracum
- The septa are saucer-like with unfolded edges
- The septal necks project backwards
- The siphuncle lies near the ventral side of the phragmocone



60 Morphology of the belemnites.

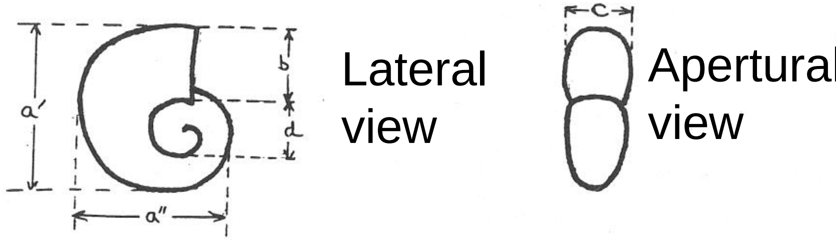
a, simplified section of the skeleton of a belemnite showing a possible reconstruction of soft parts. b, c, transverse sections across the guard in the region of the alveolus (b), and below the alveolus (c). d, e, examples of belemnites. f, *Sepia*. g, squid.



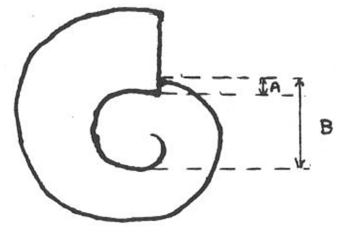
61 Belemnites with the phragmocone preserved.

a, part of a guard, fractured lengthwise along the median plane, with part of the uncrushed phragmocone lying *in situ* in the alveolus; *Belemnites oweni*, Oxford Clay, Jurassic (× 2). b, guard with anterior part of phragmocone (crushed); *Neohibolites minimus*, Gault Clay, L Cretaceous (× 2).

Measurements



a) Maximum diameter (a' and a")
b) Whorl height (b)
c) Whorl breadth (c). Can include/exclude ribs
d) Diameter of umbilicus (d)
e) Degree of involution (see below)



$\frac{A}{B} \times \frac{100}{1}$ = degree of involution, eg. $\frac{25mm}{100mm} \times \frac{100}{1} = 25\%$ Involute

Rib Counts

a) Total number in last whorl
b) Change in rib density ? Count number per 90° sector of the last whorl.

NB. Can extend rib density plot to other whorls if you wish.