Palaeontology

Practical 6

Brachiopods – Class Brachiopoda

What are brachiopods?

- Brachiopods are benthic attached (= sessile) marine animals.
- Their name literally means arm **(= brach)** foot **(= pod)**.
- Their soft parts are enclosed in a two valved shell.
- They are abundant in **Palaeozoic** and **Mesozoic** rocks and are relatively rare in the **Cenozoic** and of minor importance today
- Their size from a few millimetres to as much as 30 cm. Most measure between about 2 and 7 cm.
- They are filter feeders
- Over 3000 fossil genera are known today

Today

- Over 100 genera are living today
- They are distributed widely throughout the world in cool and temperate waters
- They are typically stenohaline (narrow range of salinity)
- they are common in eastern waters, (around Japan, South Australia and New Zealand), and a rich fauna lives in the North Atlantic.
- The British Isles have 21 species and 17 genera
- They are diverse at depths to about 500 m and a few range to greater depths down to about 6000 m.

Brachiopod morphology

- The two valves are dissimilar but equilateral
- The plane of symmetry bisects the valves across a median plane
- The shell may be calcareous or chitinous, secreted by the mantle which consists of two extensions of the body wall, one from the dorsal side and one from the ventral side of the body.
- The two valves are thus dorsal and ventral
- The brachiopod is attached to the sea-floor at its posterior end, usually by a stalk, the **pedicle**.
- The body at the posterior part of the shell, and from it the mantle lobes extend forwards to enclose a space, the mantle cavity, much of which is occupied by the **lophophore**, a feeding device which collects suspended particles.

- There is a well-developed coelom.
- The nervous and circulatory systems are not highly organised.
- The sexes are typically separate; gametes are shed into the sea, or in some cases eggs may be brooded in the mantle cavity.
- The larvae are free-swimming for a short time before they settle down on to the sea-floor and metamorphose.

- The brachiopod shell encloses the body except for the pedicle
- **pedicle valve**: The valve on the ventral side of the body, since the pedicle commonly emerges through it.
- **brachial valve**: The valve on the dorsal side, takes its name from the **brachia**, the arm-like projections of the lophophore which it carries.
- Commonly the pedicle valve is the larger, projecting at its posterior end beyond the brachial valve.
- The pedicle emerges from the shell at its posterior margin, and the opposite margin is anterior.
- The valves open slightly along the anterior margin during feeding
- Valves are attached together: in Articulata by a **hinge** of teeth and sockets; in Inarticulata by a system of muscles only.

Soft body morphology

- The mantle lines the shell
- in some groups, soft tissue extends into the shell wall by minute tubules (used in food storage and oxygen absorption).
- Small sensory bristles (setae) extend from the mantle edges.
- The body is small and the anterior two-thirds of the mantle cavity is taken up by the lophophore.
- A fleshy, lobed disc, or two coiled or folded arms called brachia each of which has a groove (**food groove**) leading to the mouth and is fringed with ciliated **filaments**.
- The cilia, by beating, maintain currents of water along three paths: a median outgoing flow, and an intake flow on either side. They also filter out minute organisms, and organic particles, from the incurrent water and these are passed, entrapped in mucus, along the food grooves to the mouth and the digestive tract.
- The intestine opens via an anus in inarticulates. In living articulates ends blindly; waste in the form of pellets is disposed of by reversing the current direction and a snapping action of the valves.

- Most brachiopocls are attached by a pedicle which is fixed to the pedicle valve by **adjustor muscles**; it is a fleshy stalk in inarticulates but is horny in articulates.
- Its distal end adheres to a rock or shell, or may diverge into rootlets to secure a hold in soft sediment (able to swivel and reorient the shell as current directions change).
- The pedicle could be reduced to a tether, could be absent and shell may be unattached, or may be cemented to a firm surface. Some extinct forms were probably anchored in soft sediment by spines.
- The opening and closing of the valves is controlled by a system of muscles which are attached close to the posterior end where they may leave **muscle scars**.

- In articulate brachiopods consists commonly of a pair of **adductor** muscles which run across the shell cavity from the interior of the pedicle valve to the interior of the brachial valve and of two pairs of **diductor** muscles which run obliquely from the pedicle valve to a projection, the **cardinal process**, from the hinge line of the brachial valve.
- The hinge line acts as a fulcrum and the cardinal process as a lever, so that as the diductor muscles contract they pull down the cardinal process and the valves open. As the diductor muscles relax, the adductor muscles contract and pull the valves together.
- Inarticulate brachiopods have a quite different and more complex system of muscles which leave only indistinct scars in the shell. As well as those which close the shell, some work obliquely to control lateral movements of the valves.

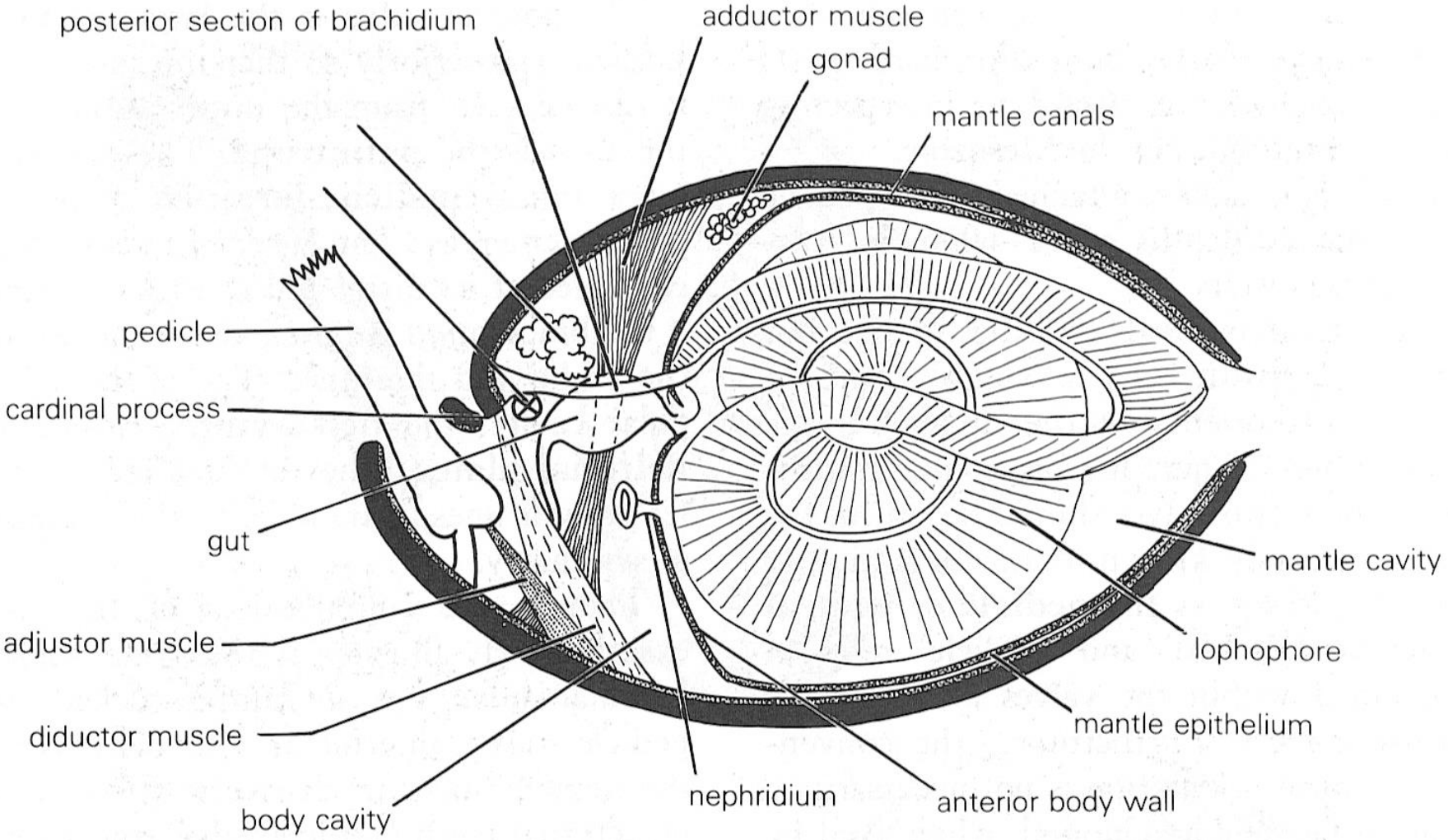


Figure 7.2 *Magellania flavescens*: median section, somewhat stylized

The lophophore

- All lophophores pass through the same early stages in development.
- The first stage, whether supported or not, is a trocholophe. Here the lophophore is merely a pair of curving 'horns' projecting horizontally on either side of the mouth and forming an incomplete ring.
- The next stage in development is the schizolophe, where the two original horns have become larger but are bent back and run parallel, directed towards the mouth.
- All brachiopod lophophores go through this stage too

- From here there are three possible developmental pathways:

a. one, starting with a **zygolophe**, which leads to a **plectolophe**: the long or short loop of many terebratulides;
b. one leading to the multilobed **ptycholophe**, as found in the modern *Lacazella*, and in some fossil strophomenides;
c. one leading to the twin spiral system of the **spirolophe**, perhaps the commonest and most widespread functional system, possessed by Recent rhynchonellides and inarticulates, as well as by fossil spiriferides and atrypides and possibly other fossil groups.

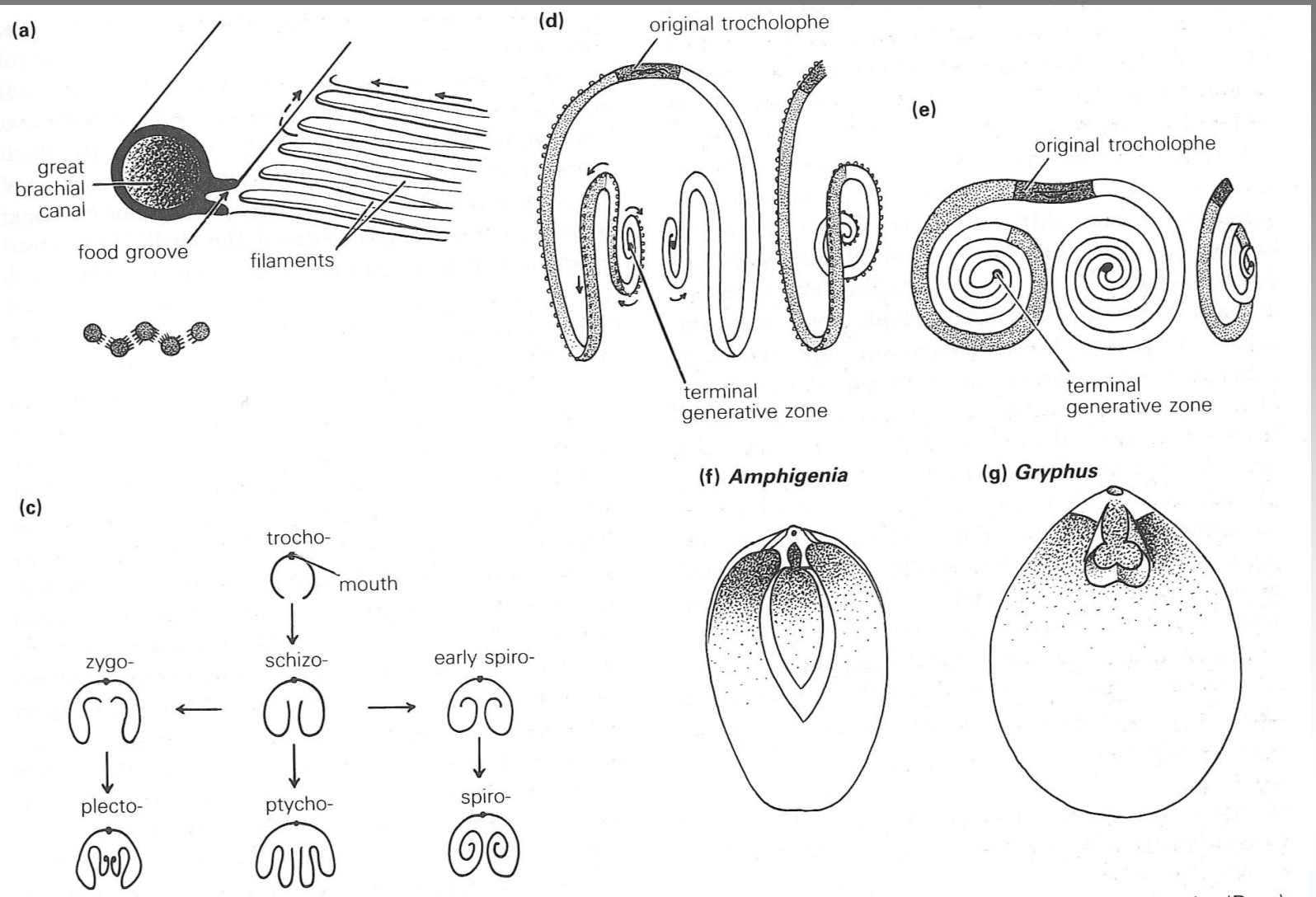


Figure 7.12 Brachiopod lophophores: (a) sectional view of lophophore with fluid-filled great brachial canal, food groove and filaments — arrows show the direction of movement of food particles; (b) arrangement of filaments in section; (c) the main types of lophophores showing various developmental pathways; (d) *Terebratula* plectolophe, showing mode of growth from a terminal generative zone; (e) *Rhynchonella* spirolophe, same; (f) *Amphigenia* (Dev.), primitive loop structure of early terebratulide (Centronellidina); (g) *Gryphus* (Rec.) short loop of Terebratulidina. [(a)–(c) redrawn from Rudwick 1970; (d), (e) redrawn from Williams and Wright 1961; (f), (g) redrawn from *Treatise on Invertebrate Paleontology*, Part H]

Shell morphology

- In inarticulate brachiopods the shell is approximately oval or circular in outline with gently convex valves.
- In articulate forms the shell may be ovate, tapering slightly at the posterior end with a short curved hinge line, or it may be semicircular in outline with a straight wide hinge line.
- The pedicle valve is typically larger than the brachial valve. Both valves may be convex, or one may be convex and the other flat or concave.
- The shell may be folded along its midline so that a ridge or fold is formed at the anterior margin of one valve with a corresponding depression or sulcus in the other. The fold and sulcus serve to keep separate the incoming and outgoing currents of water.

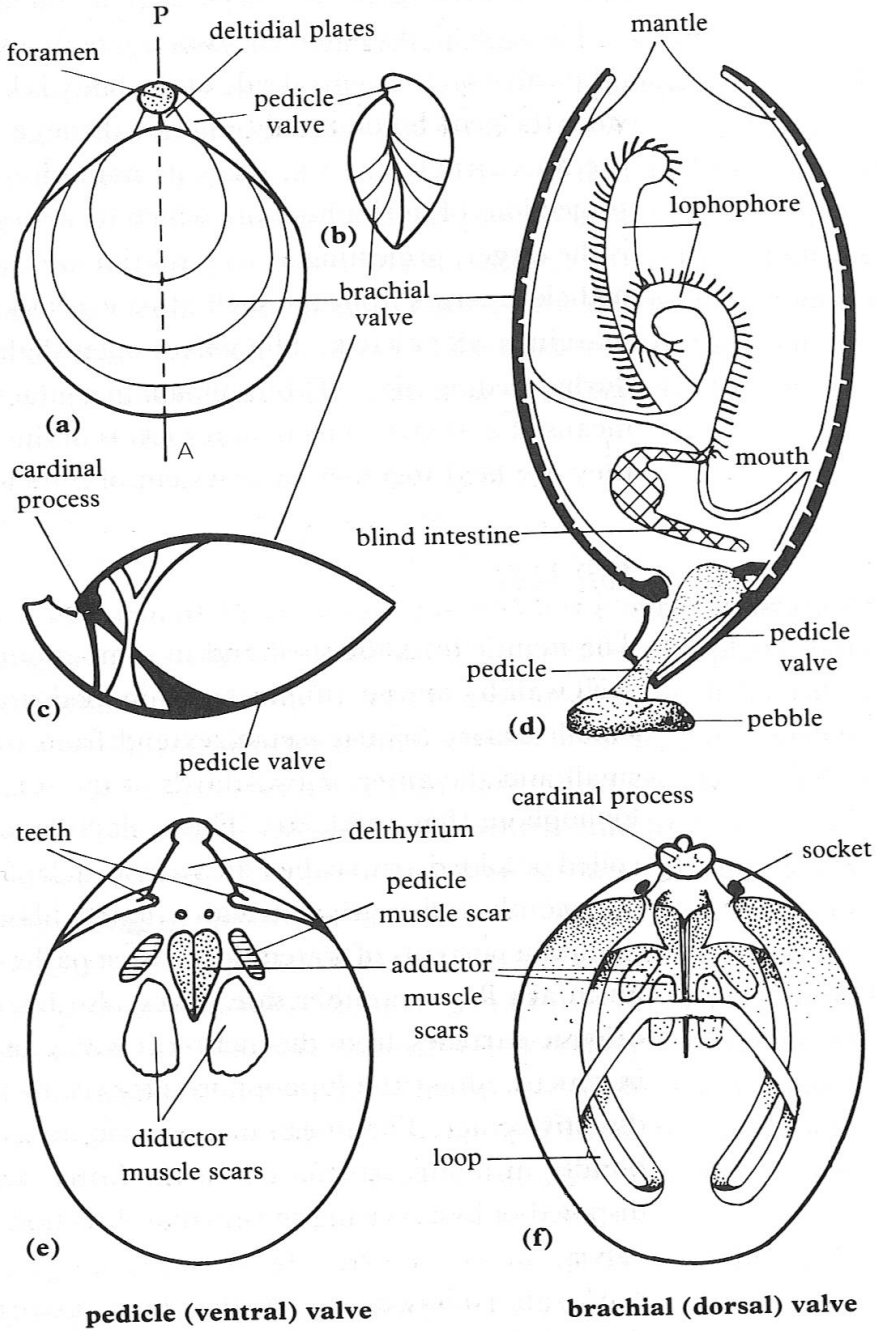
- The brachiopod shell grows by increments which form concentric growth lines on the outer surface.
- The initial shell remains at or near the posterior margin and may form the tip of a pointed **beak**. The curved convex area around the beak (in the pedicle valve), is the umbo, and in many forms a curved or flat **interarea** is interposed between it and the hinge line.
- The shell surface may be smooth or bear an ornament (concentric or radial lines, ribs, tubercles or spines) useful in distinguishing species.
- In inarticulate brachiopods the pedicle emerges through a gape between the valves, or by a groove or slit in the pedicle valve.
- In articulate brachiopods the pedicle opening, the **delthyrium**, is a triangular gap in the posterior margin of the pedicle valve. It is constricted by a pair of **deltidial plates** , or by a single plate, the **deltidium**, leaving a circular hole, the **foramen**, for the passage of the pedicle.

- The hinge apparatus consists of two **teeth** in the pedicle valve which fit into two **sockets** in the brachial valve.
- The teeth are short projections from the hinge line, one on each side of the delthyrium, and they may be supported in some genera by **dental plates** projecting from the floor of the pedicle valve. The sockets lie one on each side of a small projection, the **cardinal process**, to which the diductor muscles are attached.
- In most articulate brachiopods there are distinct muscle scars.
- In the pedicle valve, the pedicle and diductor muscle scars are grouped round two close-set adductor muscle scars.
- In the brachial valve, four adductor muscle scars are grouped on the floor of the valve, and the diductor muscle scars are on the cardinal process.
- In a small number of brachiopods the muscles are attached to the **spondylium**, in the pedicle valve. This consists of two enlarged dental plates which converge and may unite on the floor of the valve to form a V-shaped trough. It may be supported by a septum.
- In the inarticulate brachiopods are more complicated and often indistinct

- In some articulate brachiopods the lophophore is supported by a calcareous framework, the **brachidium,** a feature of systematic importance
- It arises from the hinge line of the brachial valve on either side of the cardinal process
- Brachidium forms:

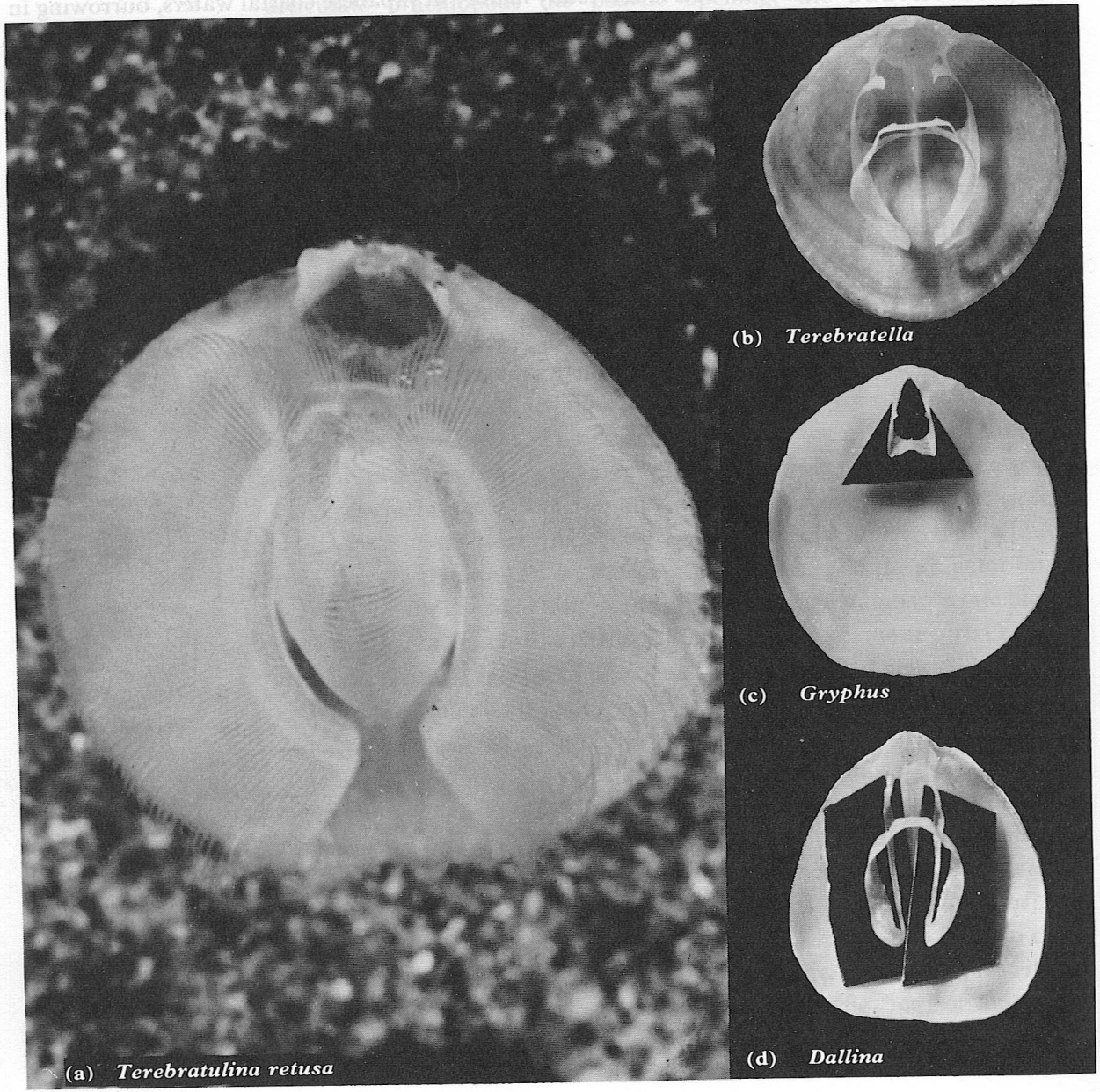
i. **crura** (sing, crus), two curved plates or rod-like processes

ii. **spiralia**, two calcareous ribbons coiled in helical spirals loops, two calcareous ribbons which unite to form a loop which may be short or longer and reflexed


P
foramen
deltidial plates
pedicle valve
(b)
brachial valve
(a)
A
cardinal process
(c)
pedicle valve
mantle
lophophore
mouth
blind intestine
pedicle valve
pedicle
(d)
pebble
teeth
delthyrium
pedicle muscle scar
adductor muscle scars
diductor muscle scars
(e)
pedicle (ventral) valve
cardinal process
socket
loop
(f)
brachial (dorsal) valve

80 Brachiopod lophophore and brachidia

a, *Terebratulina retusa*: pedicle valve removed to show lophophore extended while feeding. b–d, brachial valves with calcareous loops for support of the lophophores. (Recent shells from the Firth of Lorne; Photographs, courtesy of Dr G.B. Curry.)



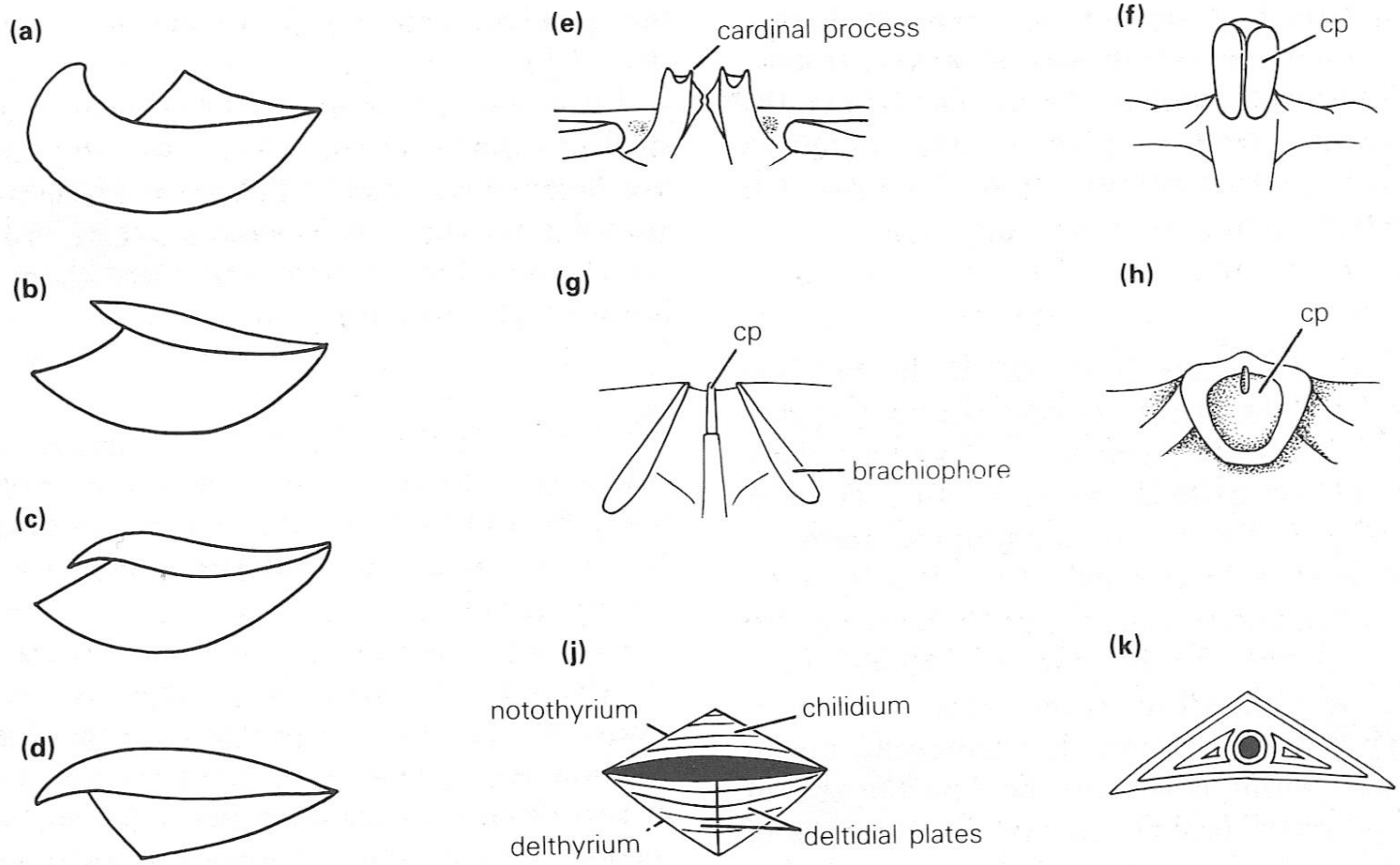


Figure 7.11 (a)–(d) Inclination of interareas: (a) brachial valve hypercline, pedicle valve anacline; (b) brachial valve anacline, pedicle valve apsacline; (c) brachial valve apsacline, pedicle valve apsacline; (d) brachial valve apsacline, pedicle valve procline; (e)–(h) Cardinal processes; (e) *Strophomena*; (f) *Pustula*; (g) *Hesperorthis*; (h) *Leptellina*; (j) pedicle foramen with closing structures; (k) Triangular stegidial plates closing delthyrium. (Redrawn from Williams and Rowell in *Treatise on Invertebrate Paleontology*. Part H)

Shell microstructure

- Brachiopod shell multilayered
- Three shell layers:

a. Periostracum (outer, non-calcareous)
b. Primary layer (middle, calcareous)
c. Secondary layer (inner, calcareous and inorganic)

periostracum

- Consists of three proteinaceous layers which underlie a gelatinous sheath
- The sheath protects the growing edge of the shell

Primary - secondary layer

- Primary layer consists of structureless crystalline calcite
- Is of constant thickness
- Secondary consists of elongated calcitic rods with rounded ends inclined at about 10^{o} to shell surface
- Keeps on growing throughout life, thus thickest towards the umbone

- In some articulate groups the shell is **punctate (or endopunctate)**, being perforated by fine tubules (with soft tissue tubular extensions the **caecae**) the **punctae**; while in other groups the shell lacks perforations or cavities and is **impunctate**.
- In one group, strophomenids, the shell is **pseudopunctate**. Here there are no tubules, but the fine structure of the secondary shell shows tiny conical deflections of inclined calcitic rods (taleolae).
- In most inarticulate brachiopods the shell has a horny appearance and is composed of alternate layers of chitin and calcium phosphate, but in a few forms it is calcareous.

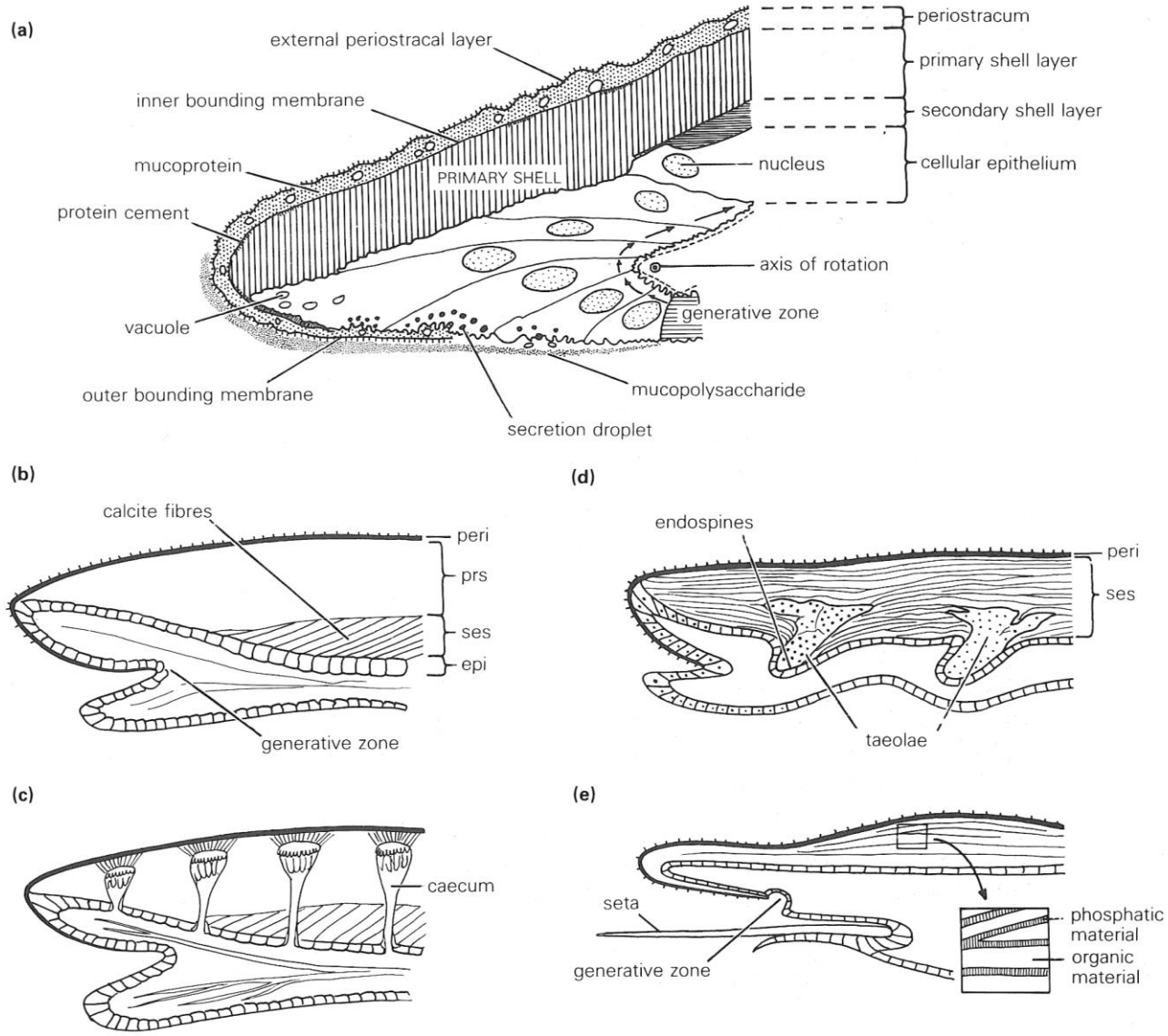


Figure 7.10 Shell structure in brachiopods: (a) standard secretory regime in *Notosaria nigricans* (for explanation see text); (b) impunctate shell (e.g. rhynchonellide); (c) endopunctate shell (e.g. terebratulide) with caecae possessing core cells freely suspended in the cavity — the secondary shell fibres are shown as cut in section; (d) pseudopunctate shell (e.g. strophomenide) with no primary layer but with taleolae prolonged internally as endospines; (e) shell of *Lingula*, with primary shell constructed of alternating layers of phosphatic and organic material — a marginal seta is shown. (Mainly based on illustrations by Williams and Rowell in *Treatise on Invertebrate Paleontology*, Part H)