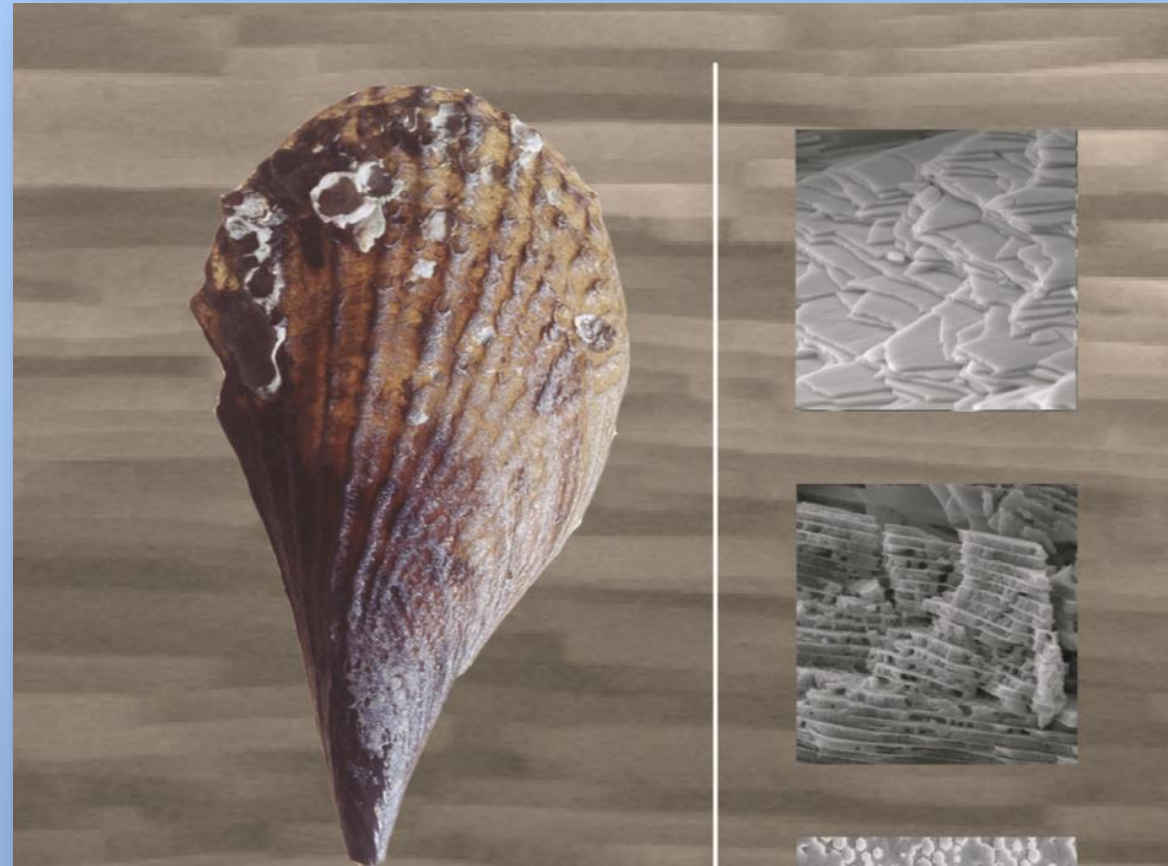


Structure, mechanics and function of the mollusc shell

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SE Marine biology



Addadi, Lia; Joester, Derk; Nudelman, Fabio; Weiner, Steve (2006): Mollusk Shell Formation: A Source of New Concepts for Understanding Biomineralization Processes. In: *Chem. Eur. J.* 12 (4), S. 980–987.



1 Introduction

1.1 Facts and classification

1.2 Body plan

1.3 Shell

2 Structure

3 Formation

4 Size

5 Shape

6 Mechanical properties

7 Varieties in structure

8 References

1.1 Facts and classification



- lat. *mollis*
- 80 000 extant species and since the Cambrian known, about 70 000 fossile species
- Concerning marine organisms, they are the largest phylum, comprising about 23 %
- They live in freshwater and terrestrial habitats and they are highly diverse, concerning size, anatomical structure behaviour and habitat.
- The scientific study of molluscs is called malacology
→ branch called conchology, which is devoted to shells.



Database World register of marine species:

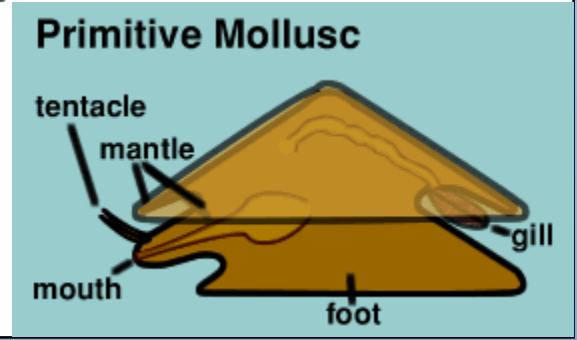
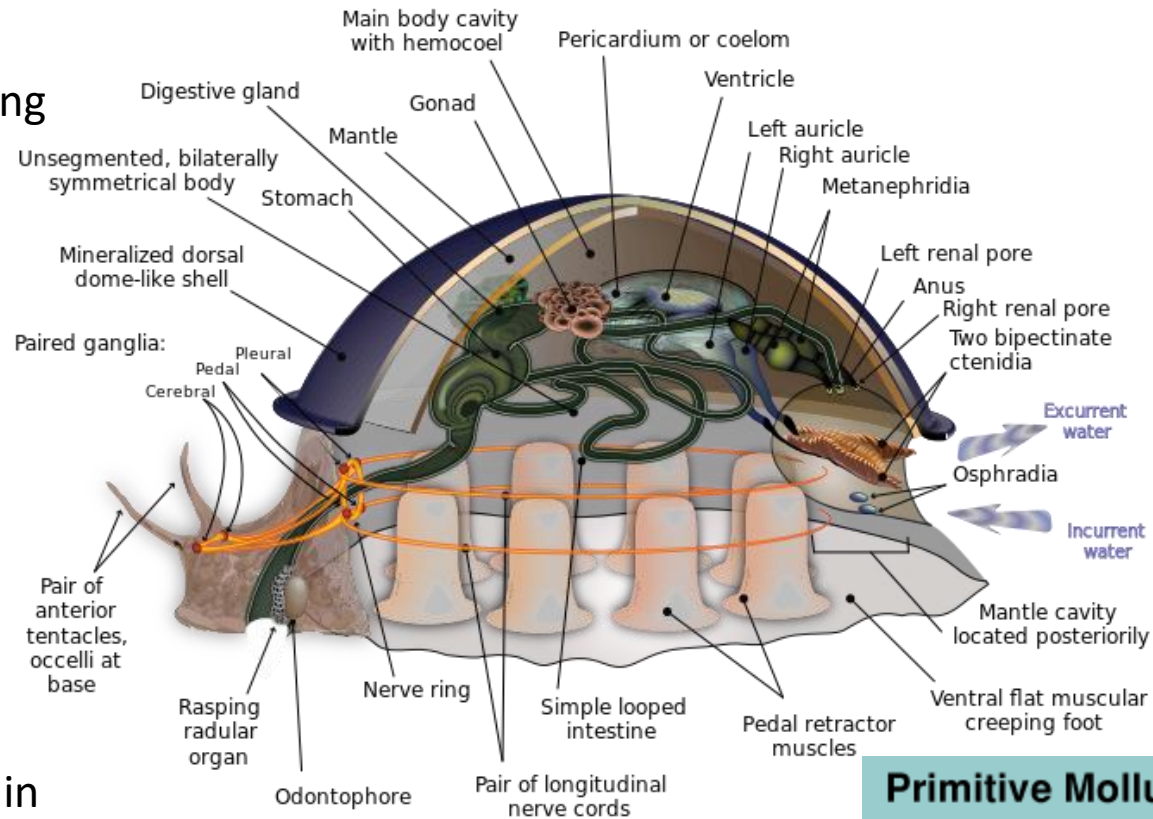
Bivalvia	Monoplacophora
Caudofoveata	Polyplacophora
Cephalopoda	Scaphopoda
Gastropoda	Splenogastres

- Cephalopoda: some characteristics remind of vertebrates
- The gastropods are the most numerous molluscs and account for approx. 80 % of the total.

1.3 Body plan



- great range of anatomical diversity among molluscs
- bilaterally symmetrical
- head, single muscular foot and visceral sac
- shell on the top which gets secreted by the mantle
 - is lined with the epidermis
- The whole soft body of the bivalves lies in an enlarged mantle cavity
 - the edge secretes the shell

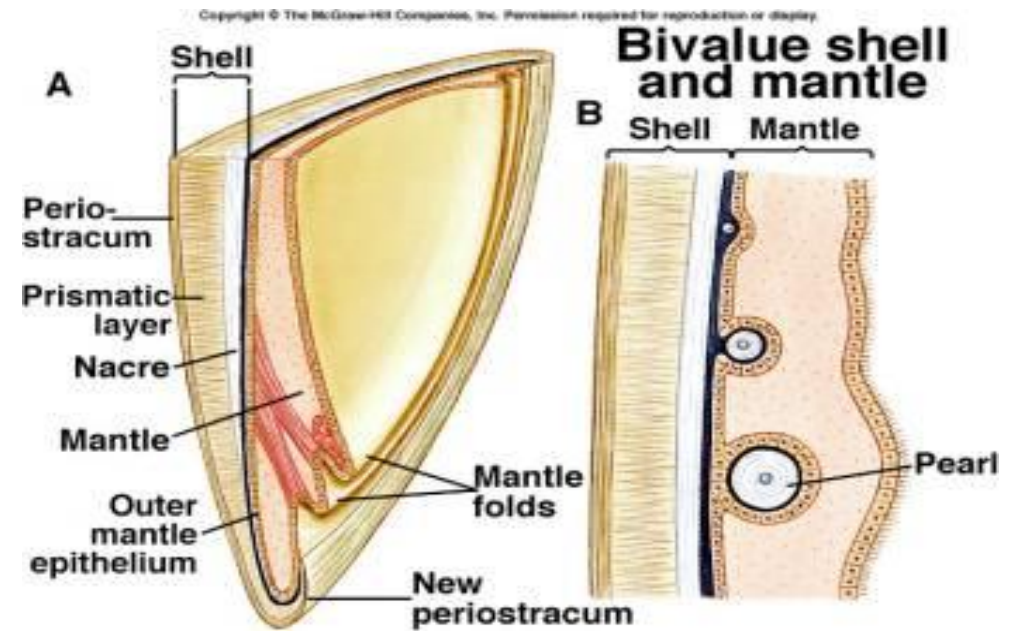




- over 100 000 living species bear a shell
- in some taxonomic groups the shell is secondarily absent
 - the squid, octopus, the caudofoveata and aplousobranchs



- Just the conchifera has the typical chalk shell
- Aplacophora has a cuticula and chalk bodies, such as scales on the surface of their back
- Polyplacophora has a cuticula and chalk bodies on the edge of their back.
- Shell layers:
 - Periostracum
 - Ostracum
 - Hypostracum
- Mantle: 3 longitudinal folds:
 - Outer: secretes prisms of chalk
 - Middle: sensory functions
 - Inner: influences the current of the water





Periostracum

- not calcified + incorporates conchiolins.
- conchiolin layer is just growing peripherally + secreted by a band of cells at the mollusc's outer edge
- protects chalk-layer from degradation + drilling organisms

Ostracum

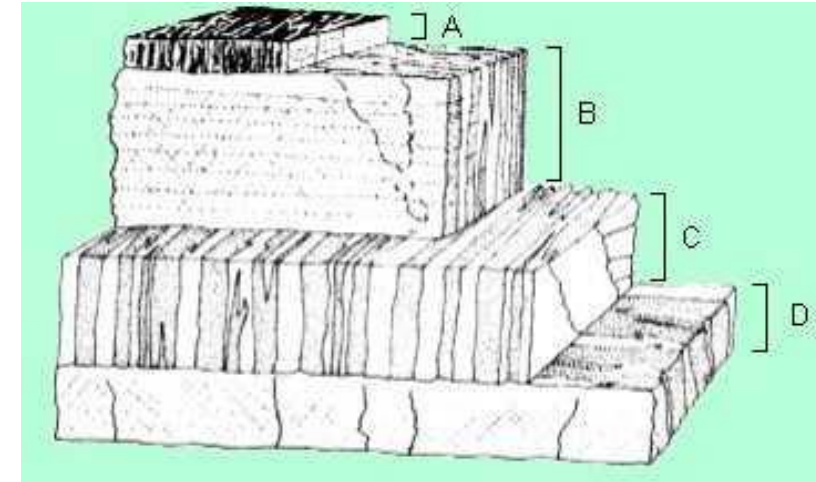
- calcium carbonate layer + build upon calcit, prismatic chalk.
- The prisms are positioned vertically to the surface + produced in a fluid layer
→ between periostracum and mantle

Hypostracum

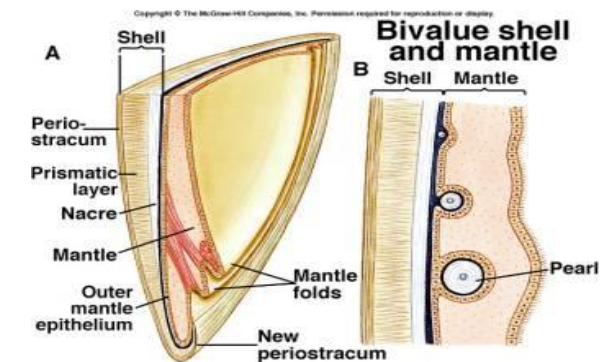
- horizontal small plates
- secreted by the whole surface of the mantle

Necrous layer:

- aragonite
- foreign substances that get between the epidermis and the shell are get coated with nacre + injuries of the nacre-secreting epithel
- created by the epithelial cells of the mantle tissue



http://www.gireaud.net/us/coquille_us.htm

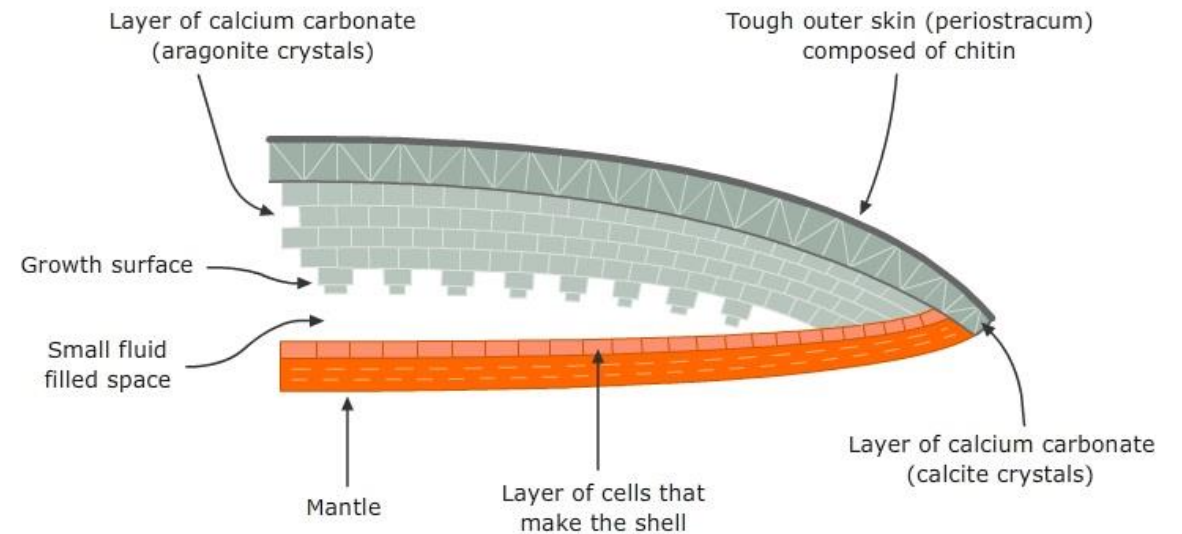


3 Formation



- Mantle:
 - extends exactly beyond the shell aperture
 - the edge adds a shell increment to the aperture margin, which forms a „growth line“
- Simplified: the shell is kind of a secretion product of the surface of the mantle
- not involved in the metabolism

Structure of a typical mollusc shell

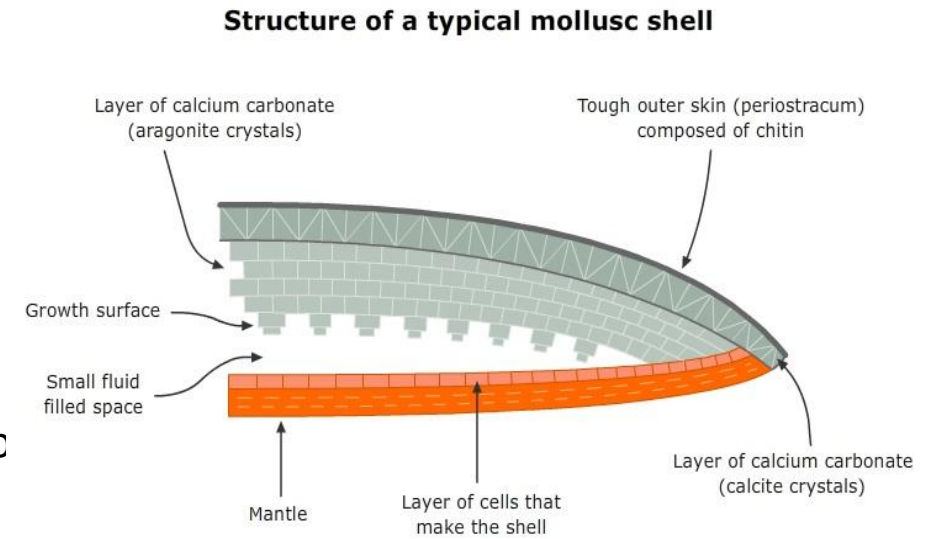


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The increment that is secreted has 2 components:

- organic component is made up of polysaccharides and glycoproteins
- The outer layers of carbonate can be suspended from the periostracum
 - accumulation of ions that are responsible for crystallization
- pumped by ion pumps in the calcifying epithelium
- calcium ions are derived from the environment by the gills, the gut and the epithelium
- haemolymph transports the calcium ions to this calcifying epithelium and stores them as granules in the cells
- pumped into the extrapallial space



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Genes and TF

Engrailed:

demarks the edge of the shell field

Decaplentaplegic (Dpp):

controls the shape of the shell

Hox1 and Hox4:

thought to be responsible for the start of mineralization

Perlucin:

increases the rate at which calcium carbonate precipitates to form a shell

Perlustrin:

is responsible for the elasticity of organic layers and thus it helps nacre to stay so resistant to cracking

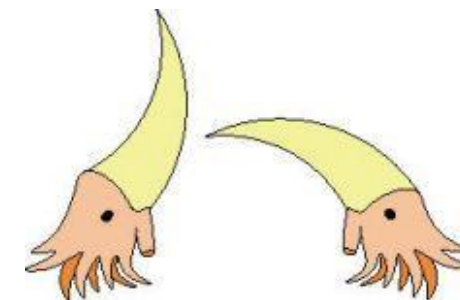


- The shell is mostly large enough to cover and protect all the soft parts from predation and dessication.
- In the case of gastropod molluscs, the shell is often reduced and just protects the visceral mass.
→ e.g. *ophistobranchs* and some *pulmonates*
- The slugs have an internal shell, internal chalk granules or no shell at all.



- controlled by TFs and by developmental rate
- Gastropods:
 - shell tube coils in a logarithmic spiral + isometric proportions
 - length, area and volume parameters as it grows.
 - columella: form the axis of shell coiling
- Bivalves:
 - changes through growth, but the pattern of growth stays constant.
- genetic feature.
 - clones of gastropods can develop different shell morphologies.

- univalved molluscs:
 - Endogastric shells coil backwards
 - Exogastric shells coil forwards
- Bivalves:
 - opisthogyrate
 - prosogyra



Exogastric

Endogastric

<http://www.tonmo.com/community/pages/morphology/>



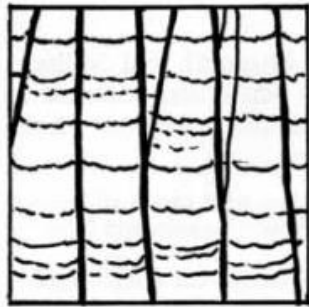
Wainwright (1969):

„...the mechanical function of the shell depends upon its ability to resist deformation and failure under environmental stress.“

Prismatic microstructures

simple prismatic structure

- consists of column-shaped crystals
- 200 μm length and 9-80 μm in width
- Additionally they are aligned normal to the shell exterior
- as an outer shell layer

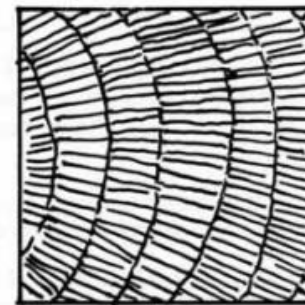


a

Taylor, John D., and M. Layman. "The mechanical properties of bivalve (Mollusca) shell structures." *Palaeontology* 15.7 (1972): 5.

composite prismatic structure

- consists of very small needle-like crystals
- 2 μm width and up to 10 μm in length
- radiating from a central axis, which is aligned parallel to the shell exterior
- as an outer shell layer



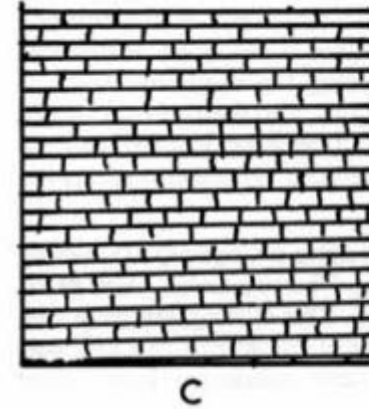
b

Taylor, John D., and M. Layman. "The mechanical properties of bivalve (Mollusca) shell structures." *Palaeontology* 15.7 (1972): 5.

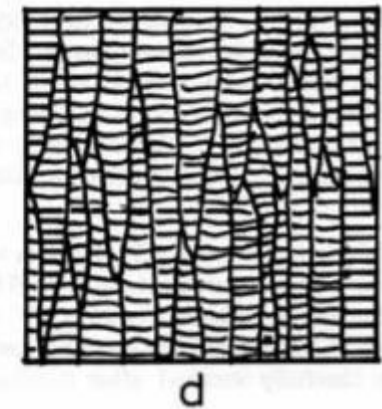


- tablet-like crystals
- 2-10 μm in length and 0,4-3 μm in thickness
- arranged in sheets (brick-wall)
- Another type:
crystals arranged into columns (**lenticular nacre**)
- in middle and inner layers of shells
- strongest form of microstructure in tension, compression and bending.

Sheet nacre



Lenticular nacre



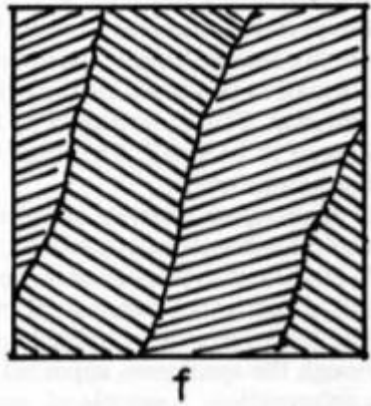
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Crossed microstructures

simple crossed lamellar microstructure

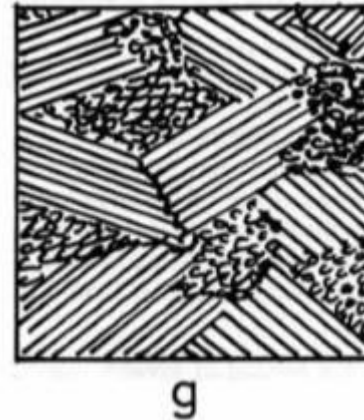
- lath-like crystals that are arranged into the lamellae
- 5 μm in width and up to 20 μm in length



Taylor, John D., and M. Layman. "The mechanical properties of bivalve (Mollusca) shell structures." *Palaeontology* 15.7 (1972): 5.

complex crossed lamellar microstructure

- similar to the other type
- intergrowth of blocks of crystals

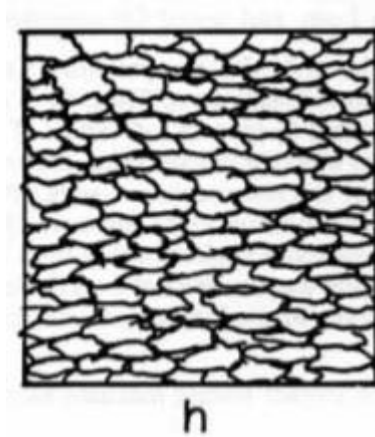


Taylor, John D., and M. Layman. "The mechanical properties of bivalve (Mollusca) shell structures." *Palaeontology* 15.7 (1972): 5.



Homogenous structure

- small granular crystals with no typical crystal form
- 5 μm in diameter
- Buggild (1930): „*in ordinary light we see no structure at all*“
- no other specific elements than tiny granules it is homogenous.



Taylor, John D., and M. Layman. "The mechanical properties of bivalve (Mollusca) shell structures." *Palaeontology* 15.7 (1972): 5.



- size of the largest microstructural units
- crossed lamellar structure consists of small crystals
- nacre and homogenous structures have much smaller crystals
- small cracks in the tiny crystals would waste their energy
- tendency for cracks along the boundaries of the larger units in crossed lamellar and prismatic structures
- tension, compression and bending
- shell material is from 3 to 23 times stronger in compression than in tension
→ easier to break them by pulling than by breaking.

7 Varieties in structure



- **Monoplacophora**

- bricklike crystals of aragonite are formed like layered sheets
- foliated aragonite is thought to have evolved from the nacreous layer



- **Chitons**

- 8 overlapping valves out of chalk, surrounded by kind of a belt



- **Gastropods**

- in some marine species: periodic resting stages where the shell does not increase
- in overall size, but a more thickened and strengthened lip is produced instead
- thickened areas are called *varices*



- **Cephalopods**

- external shell
- Cuttlefish, squid, spirula and vampire squid have small internal shells



- **Scaphopods**

- hollow, and open at both ends

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<http://prettyspoiled.com/2013/06/05/ea-shell-beauty-look/>

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