_seminario 25 giugno 2013

I macroforaminiferi del Paleogene:
classificazione, biostratigrafia e paleoecologia

ISPRA
Istituto Superiore per la Protezione e la Ricerca Ambientale
SERVIZIO GEOLOGICO D'ITALIA
Organo Cartografico dello Stato (legge N°68 del 2-2-1960)
Dipartimento Difesa del Suolo

SAPIENZA
UNIVERSITÀ DI ROMA

ORDINE DEI GEOLOGI DEL LAZIO

Introduzione alla paleobiologia dei macroforaminiferi

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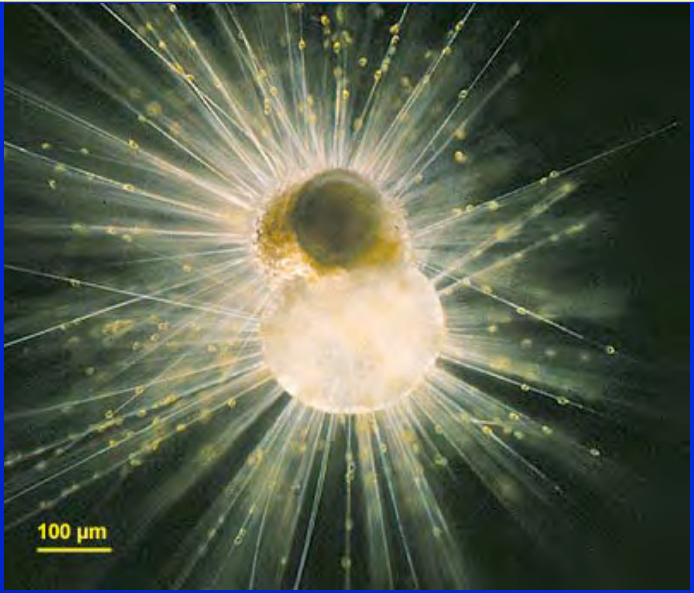
Outline

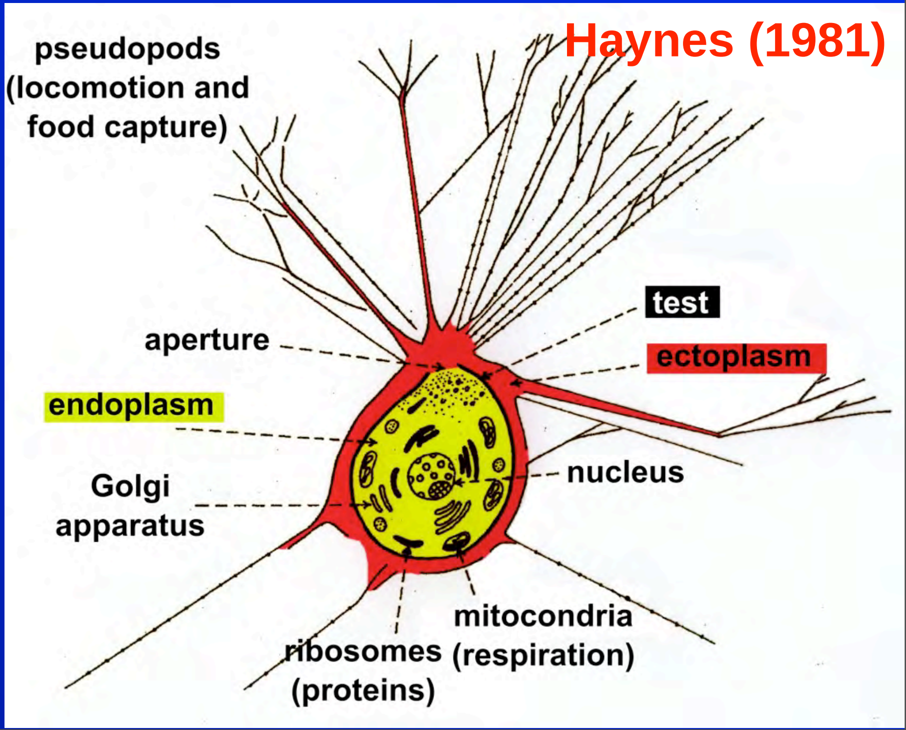
- What are foraminifera?
- What are larger foraminifera (LF)?
- LF: a long history
- Reproduction and dimorphism in LF
- Symbiosis in LF

What are foraminifera?

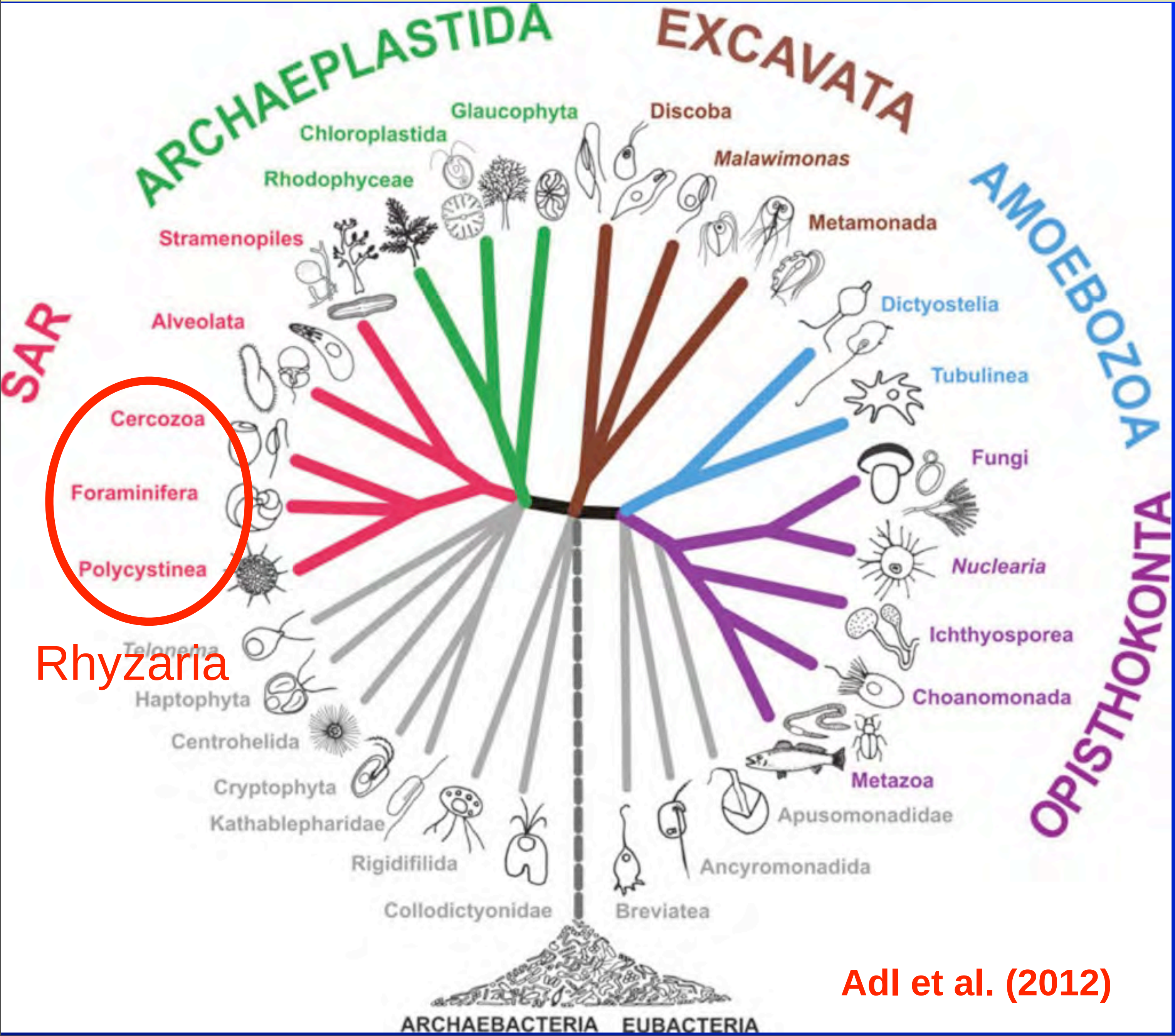
Foraminifera are an exceedingly diverse group of unicellular organisms ("Protista"), with estimated 3-4,000 (Murray, 2007) to 10,000 (Sen Gupta, 2003) modern species; the known fossil species are about 30,000 (Murray, 2007).

They have a shell (= test) that consists of one or more chambers, communicating through orifices called foramina.
The chambers are separated from each other by partitions called septa.
The last chamber communicates with the exterior through one or several apertures. Cytoplasm that completely fills all the chambers emerges through these exterior apertures and covers the outside of the test where it emits fine filamentous granular and reticulate pseudopodia (Bellier et al., 2010).



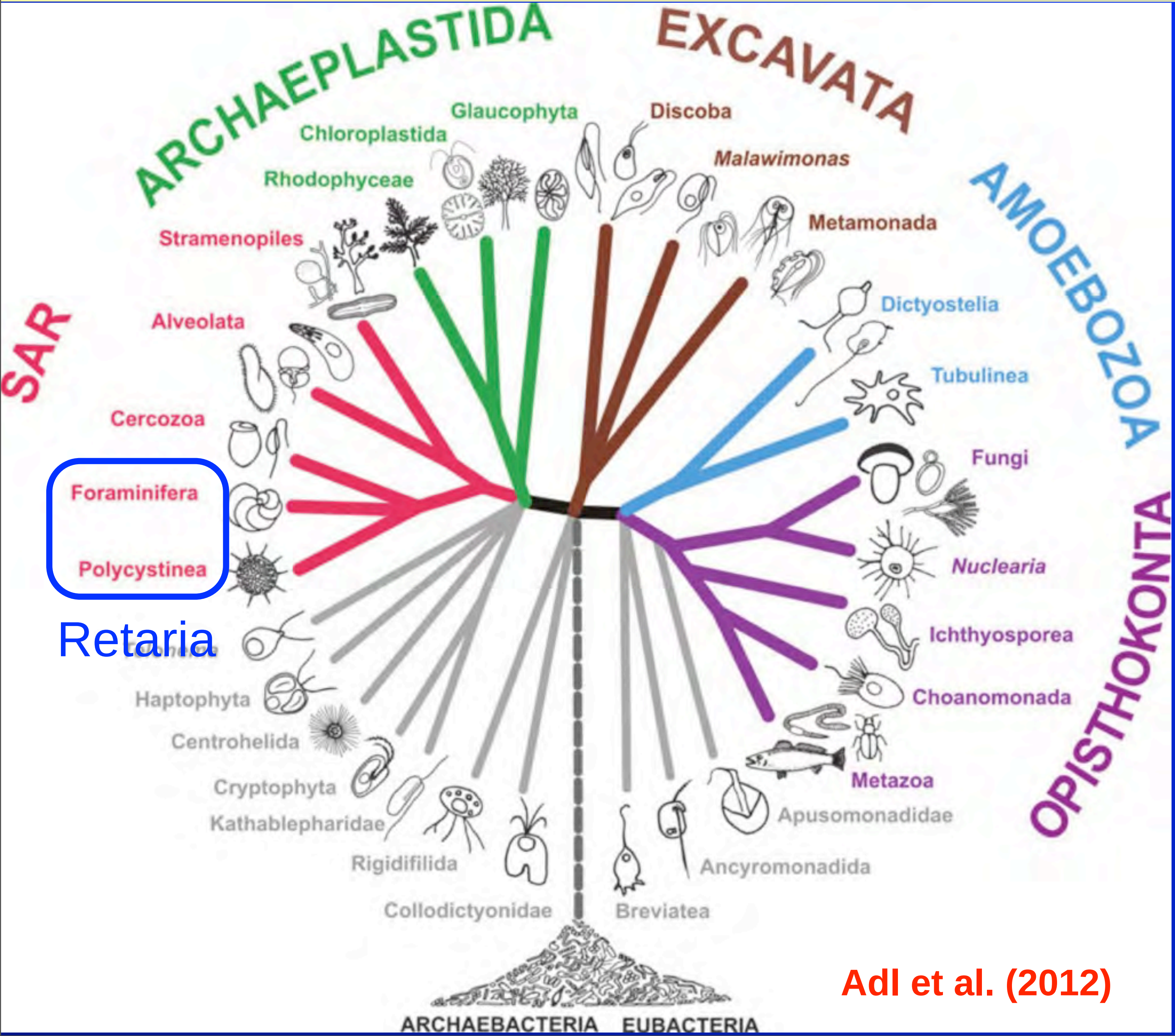

Haynes (1981)

What are foraminifera?



Adl et al. (2012)

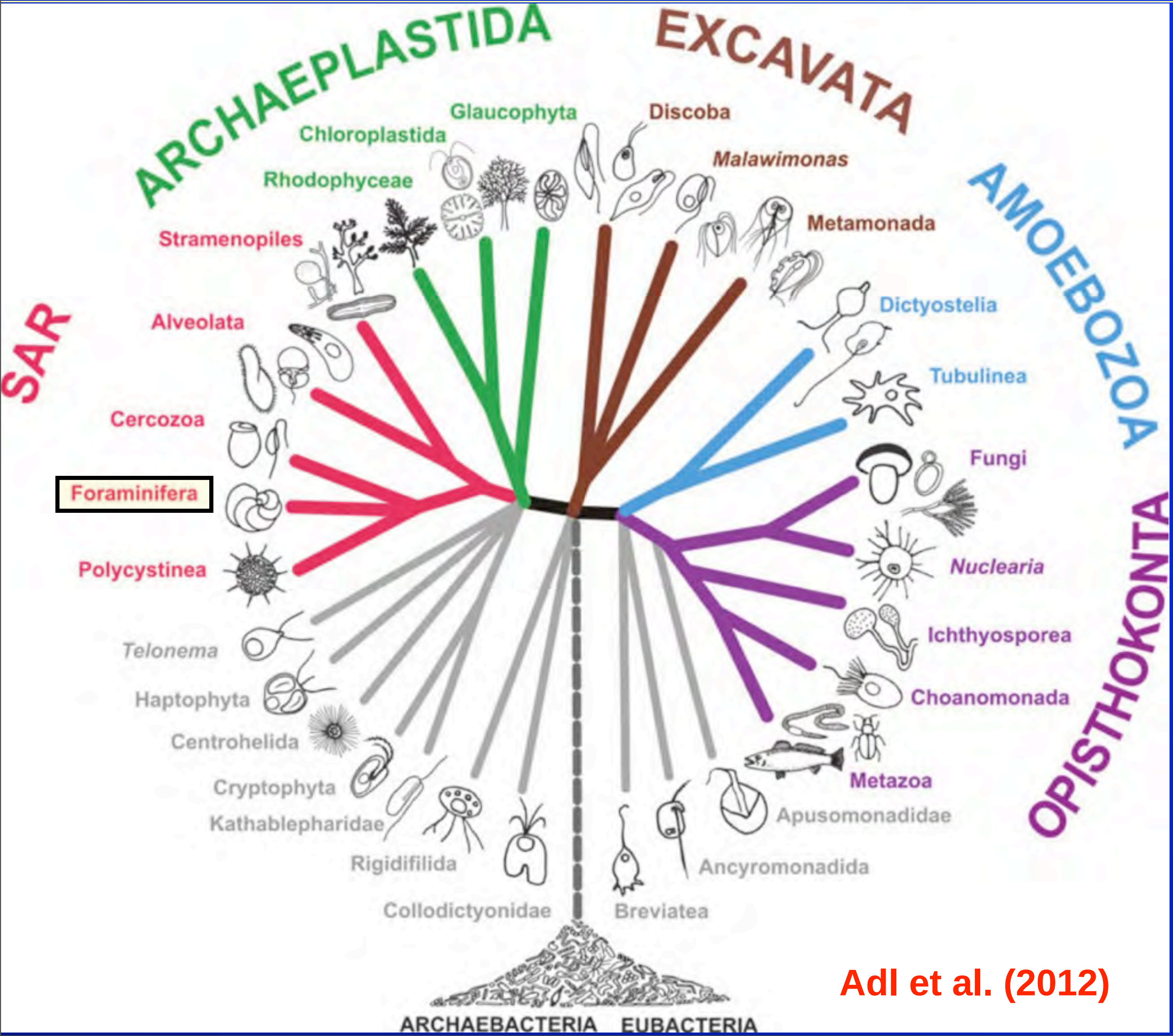
What are foraminifera?



Retaria

Adl et al. (2012)

What are foraminifera?



Adl et al. (2012)

What are foraminifera?

Loeblich & Tappan (1987):

Order **FORAMINIFERIDA**

1) Suborder **ALLOGROMIINA**
2) Suborder **TEXTULARIINA**
3) Suborder **FUSULININA**
4) Suborder **INVOLUTININA**
5) Suborder **SPIRILLININA**
6) Suborder **CARTERININA**
7) Suborder **MILIOLINA**
8) Suborder **SILICOLOCULININA**
9) Suborder **LAGENINA**
10) Suborder **ROBERTININA**
11) Suborder **GLOBIGERININA**
12) Suborder **ROTALIINA**

What are foraminifera?

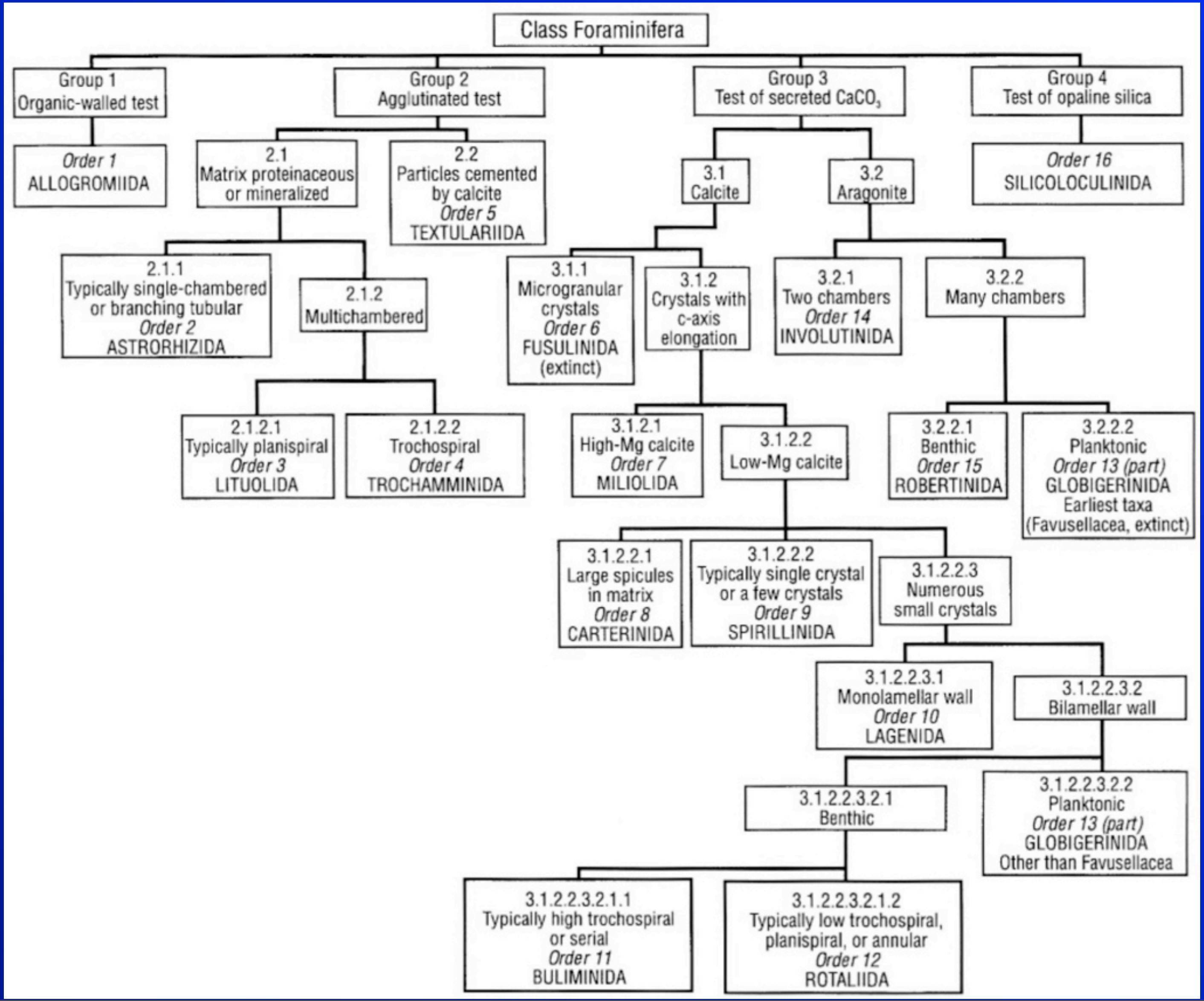
Sen Gupta (2003):

Class **FORAMINIFERA**

1) Order **ALLOGROMIIDA**
2) Order **TEXTULARIIDA**
3) Order **ASTRORHIZIDA**
4) Order **LITUOLIDA**
5) Order **TROCHAMMINIDA**
6) Order **FUSULINIDA**
7) Order **INVOLUTINIDA**
8) Order **SPIRILLINIDA**
9) Order **CARTERINIDA**
10) Order **MILIOLIDA**
11) Order **SILICOLOCULINIDA**
12) Order **LAGENIDA**
13) Order **ROBERTINIDA**
14) Order **GLOBIGERINIDA**
15) Order **BULIMINIDA**
16) Order **ROTALIIDA**

What are foraminifera?

Sen Gupta (2003):



What are larger foraminifera?

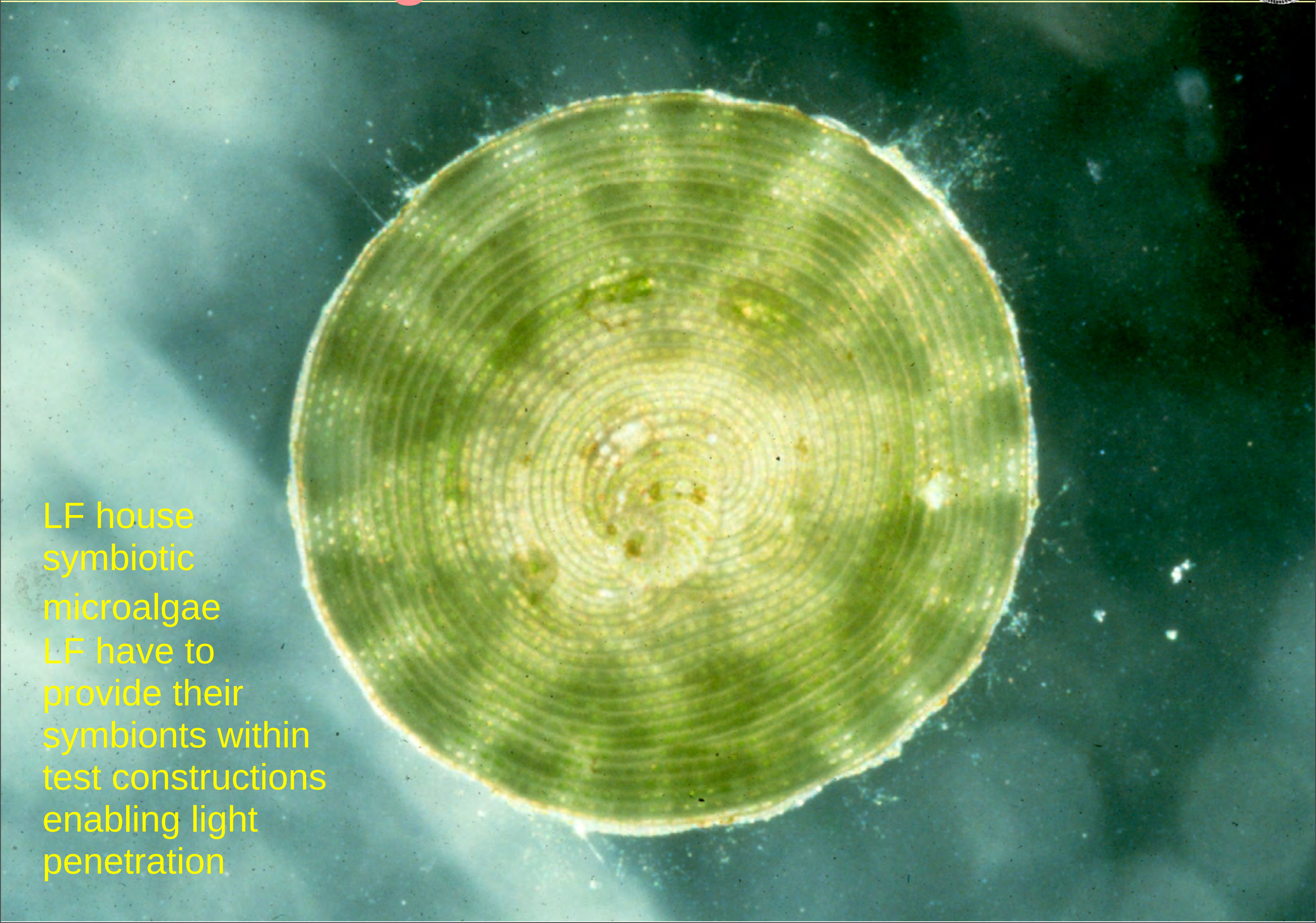
Larger (Benthic) Foraminifera (LF) commonly exceed 3 mm^3 in volume and have complex internal morphologies (Hallock, 1985).

The diameters of LF tests are usually between 1 mm and >10 cm, whereas the “normal” smaller foraminifera diameters are 0.2 to 0.6 mm on the average.

What are larger foraminifera?

- larger than 1 mm
- sometimes 1 cm to 2 cm
- the largest today up to 13 cm!

What are larger foraminifera?

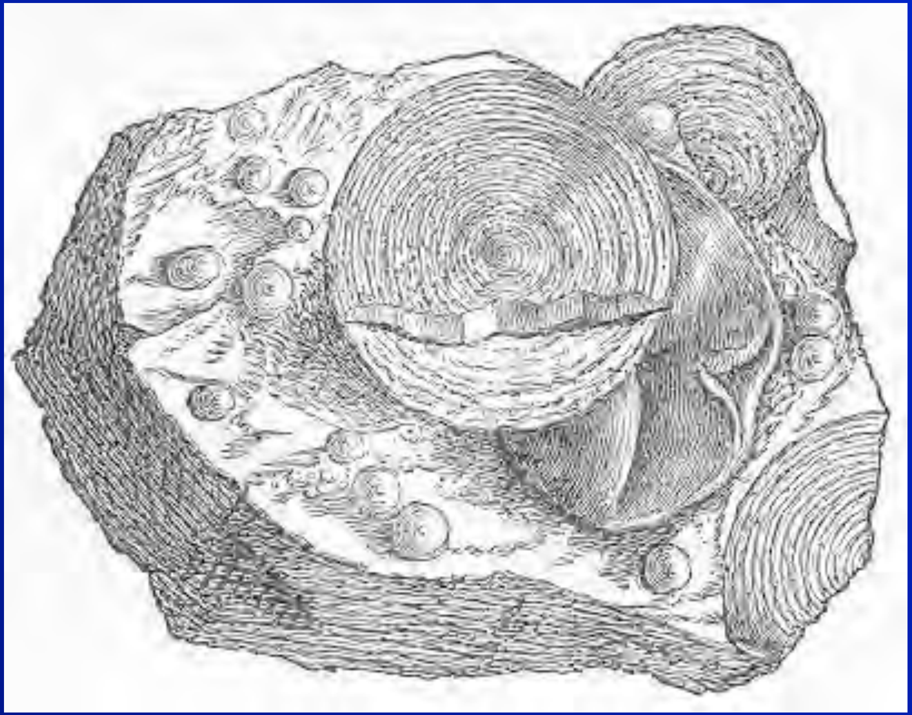


LF house symbiotic microalgae

LF have to provide their symbionts within test constructions enabling light penetration

LF: a long history

Strabo (Geographica, book xvii, cap. i, 34) was probably the first to record the existence of (larger) foraminifera: he affirmed that the Egyptian Nummulites were the petrified remains of beans left behind them by the builders of the Pyramids, in spite of the explicit statement of Herodotus (Euterpe, ii. 37) that the Egyptians never grew or ate beans in any form (Heron-Allen, 1915)



Piece of nummulitic limestone from the Great Pyramid of Gizeh (after Nicholson, 1877).

LF: a long history

“IN the Dawn of History the Tartars in their flight before the victorious army of Ladislaus, King of Transylvania, scattered money as they fled, trusting to the apparently already established instincts of the Teuton soldiers that their pursuit would be thereby arrested. But King Ladislaus prayed that this money might be turned into stones, and his prayer was immediately granted. Hence the Nummulites” (Heron-Allen, 1915)

Ladislaus IV of Hungary (1262-1290)

Reproduction/dimorphism in LF

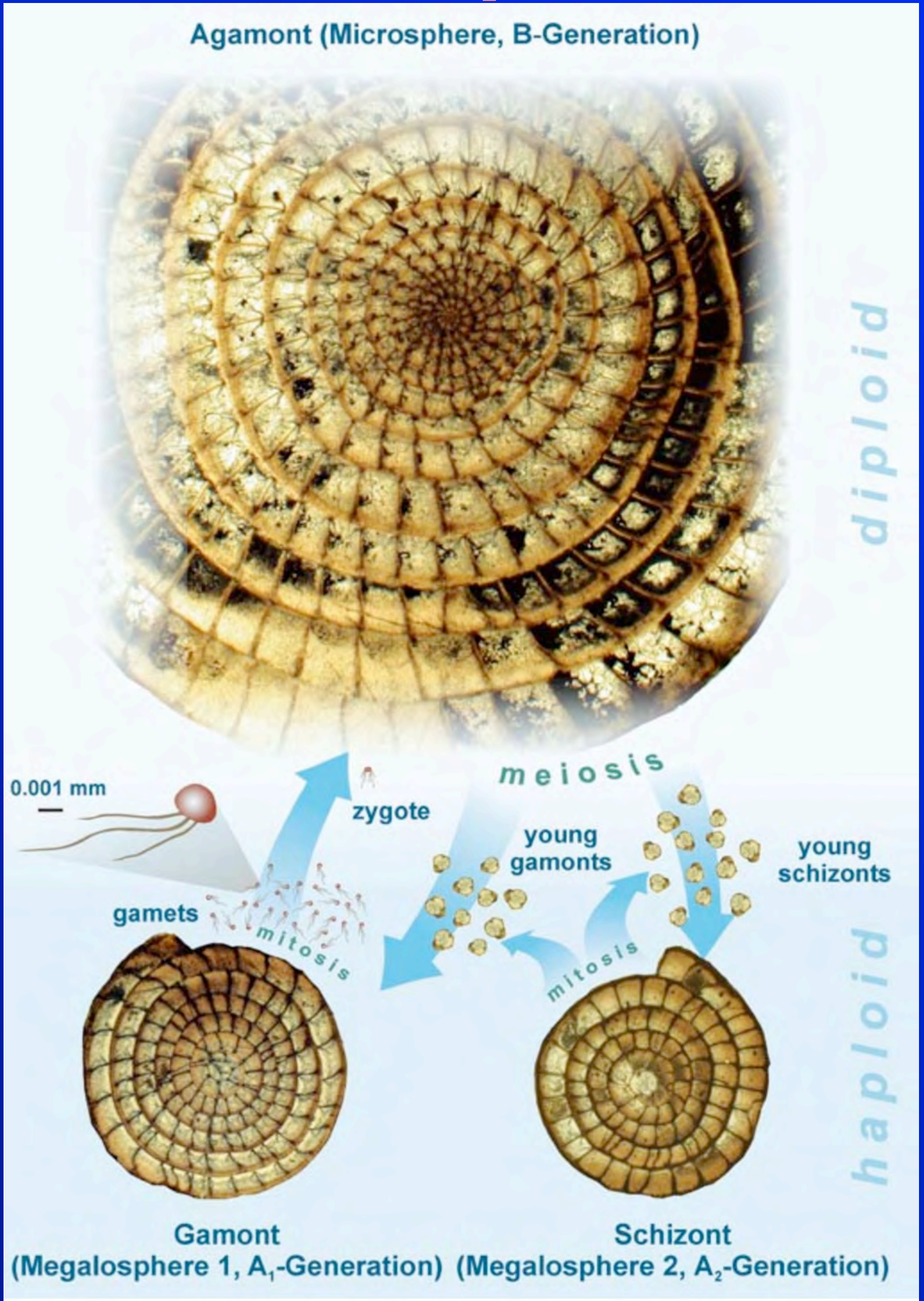
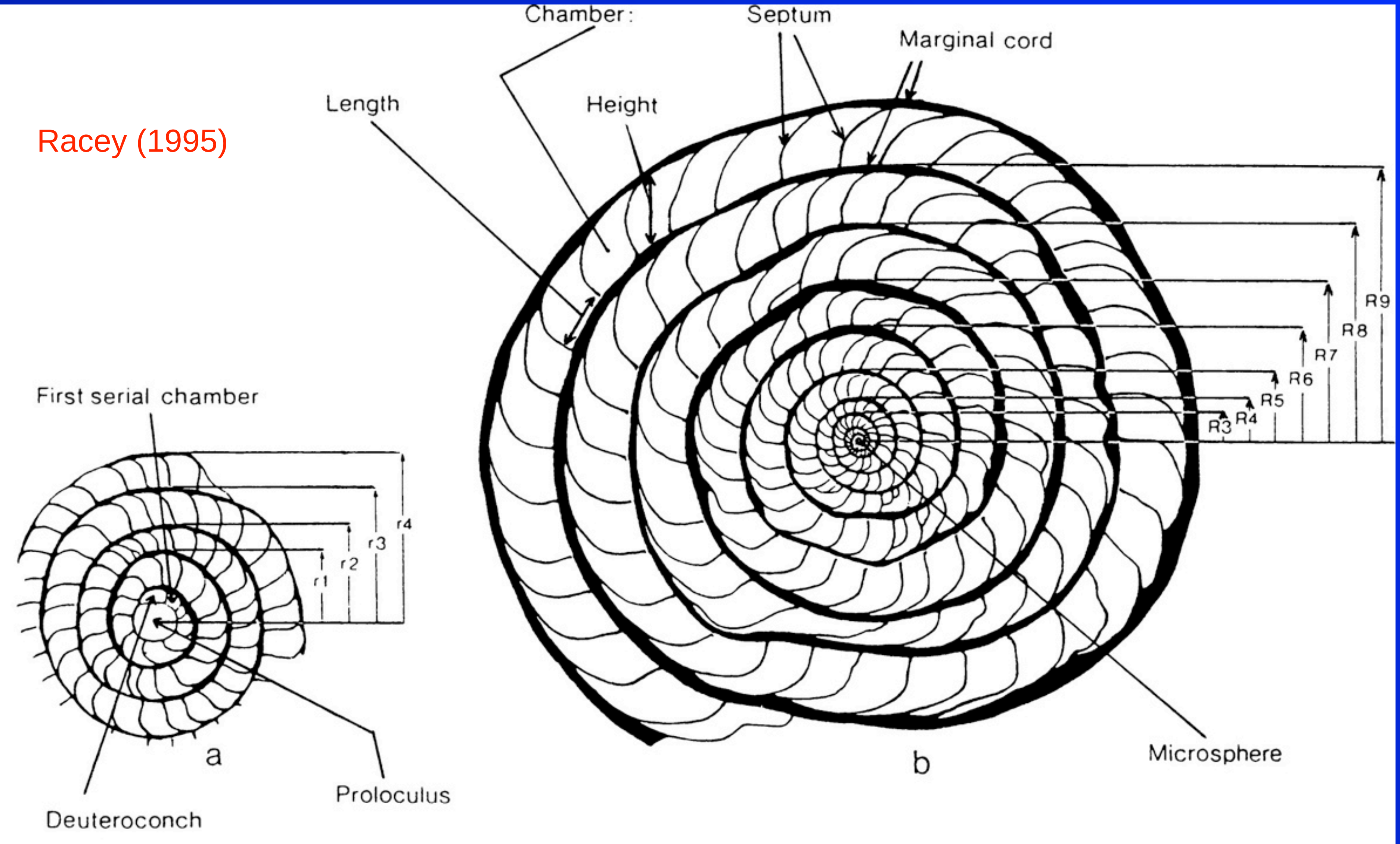


Figure 3 The life cycle in larger foraminifera (size of gametes not to scale)

Hohenegger (2011)

Reproduction/dimorphism in LF

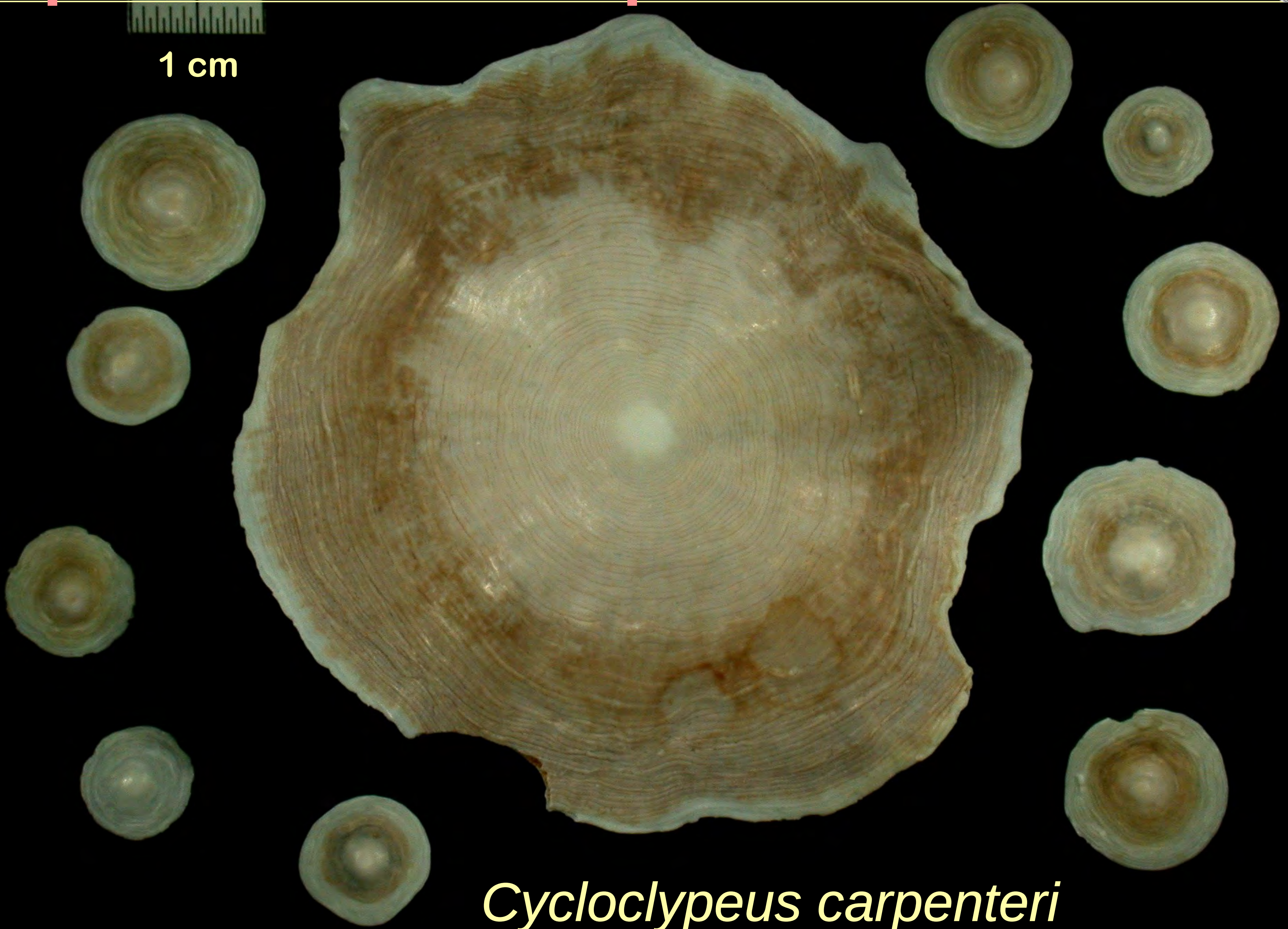
Racey (1995)



TEXT-FIGURE 18

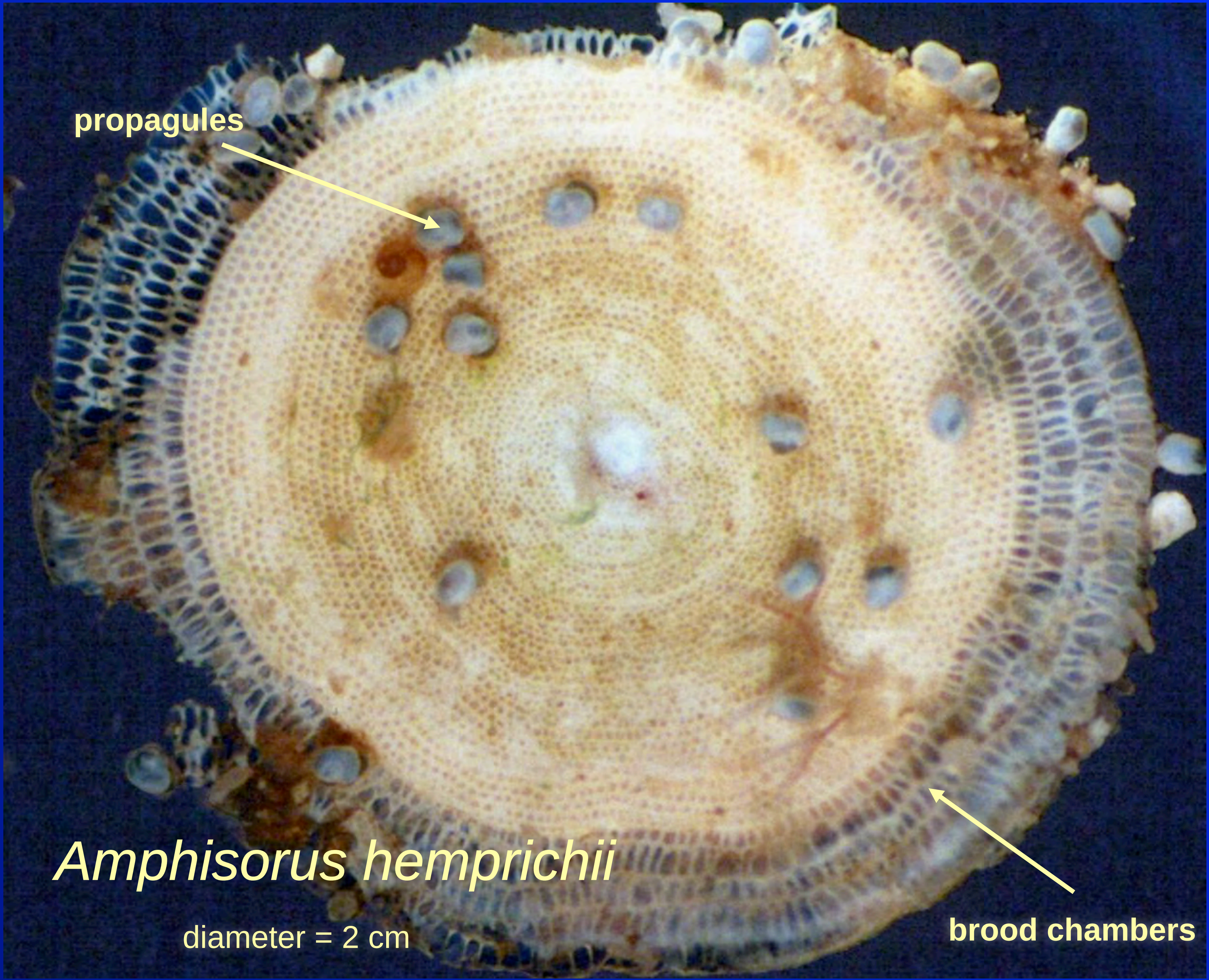
Equatorial sections of *Nummulites* A-Form (a) and B-Form (b) ×10, showing the method of measurement of the radius per whorl.

Reproduction/dimorphism in LF



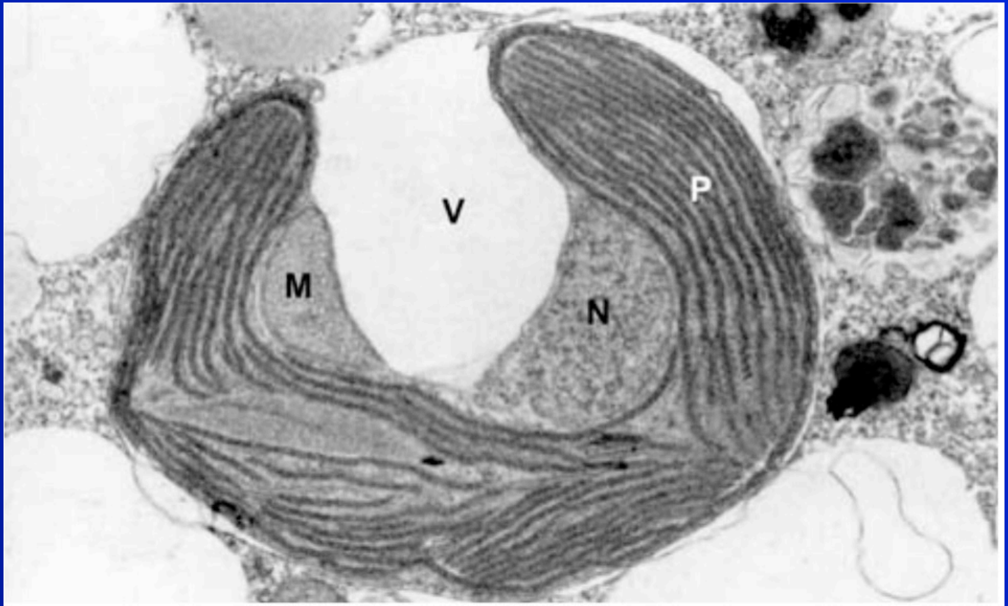
Cycloclypeus carpenteri

Reproduction/dimorphism in LF



Symbiosis in LF

Several foraminifera, in particular planktonic forams and LF, host symbiotic algae inside their cytoplasm.



Transmission electron microscope (TEM) image of a symbiotic microalgae (size = 0.0048 mm) within a foraminiferal cell. The chloroplast (P) responsible for photosynthesis surrounds the nucleus (N) and the mitochondrium (M). A large vacuole (V) is typical for storing the products of photosynthesis like glycerols and lipids (from Leutenegger 1984).

Hohenegger (2011)

The foraminifer *Planostegina* (size = 3 mm) from 90 m depth with retracted protoplasm, which is colored by symbiotic microalgae.

Hohenegger (2011)

Symbiosis in LF

For this reason, symbiotic forams could be compared to zooxanthellate corals, having similar ecological requirements.

Nutrients and K-strategy

Hottinger (1997)

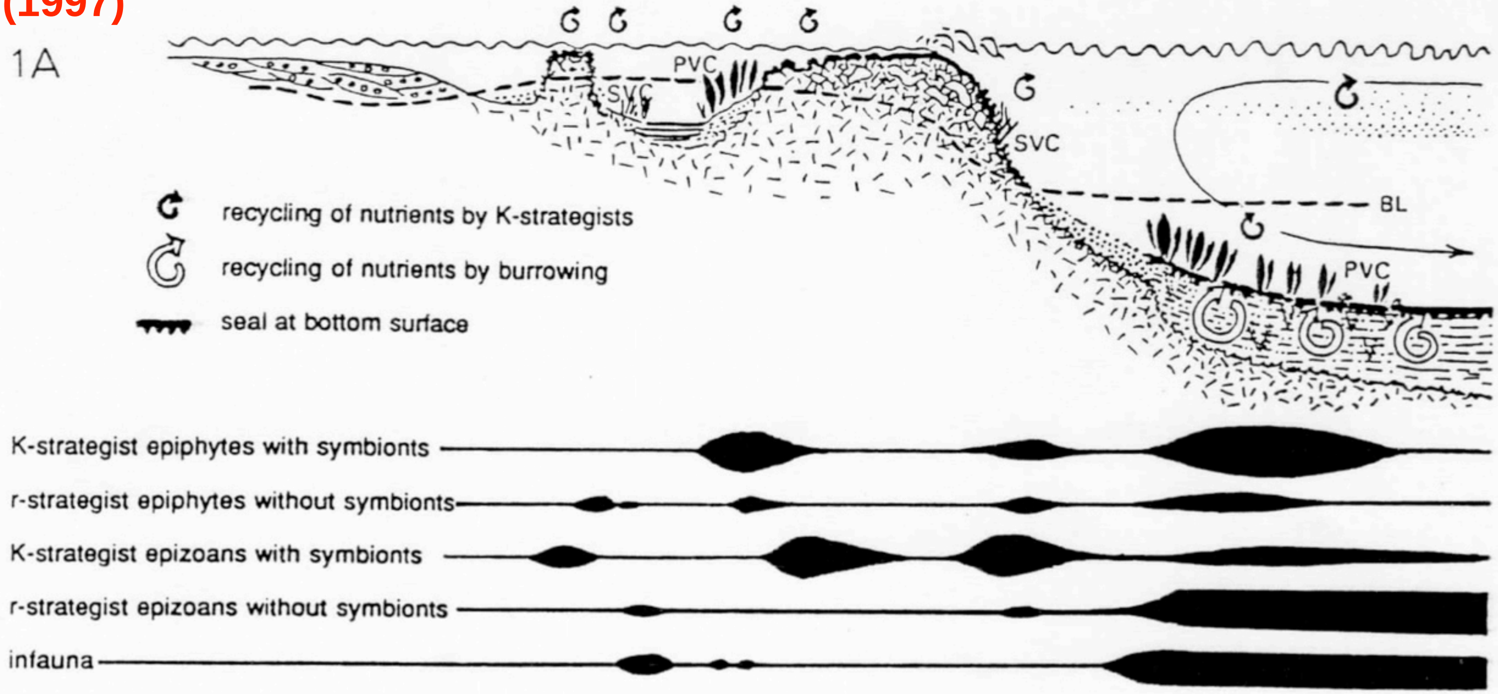
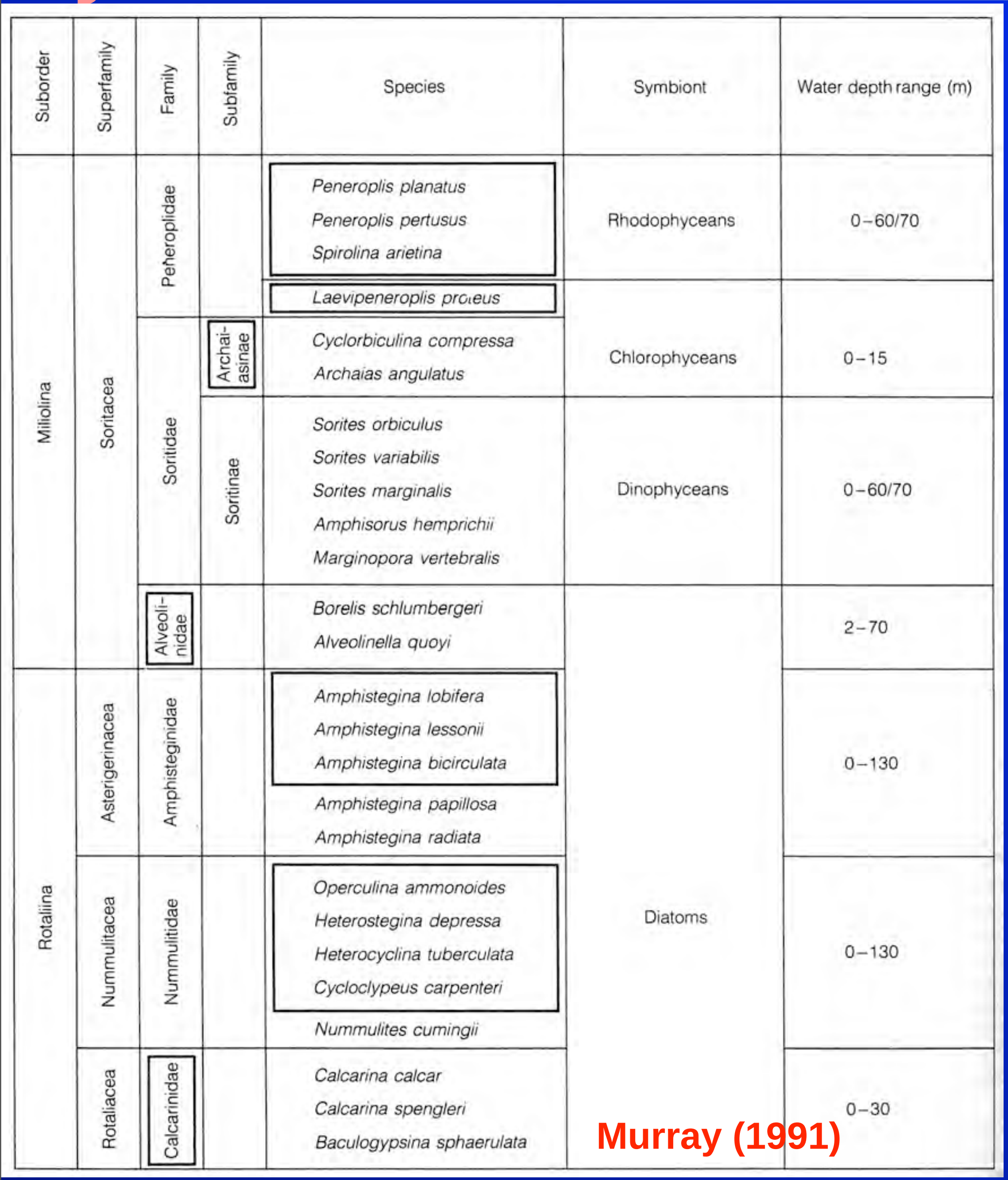


FIG. 1A. – Distribution of r– and K-strategist foraminifera in an oligotrophic, tropical, shallow sea with antiestuarine circulation. Cartoon showing the location of the main nutrient recycling processes. Note the discontinuities in space of the K– and r-dominated assemblages. Only the K-strategists depend, by their symbiotic relationship, on light and produce bathymetric markers. PVC : permanent vegetation cover on soft bottom. BL : base level of coarse sand and pebbles marking the lower limit of frequent high water energy events hampering the growth of long-living K-strategists.

Symbiosis in LF

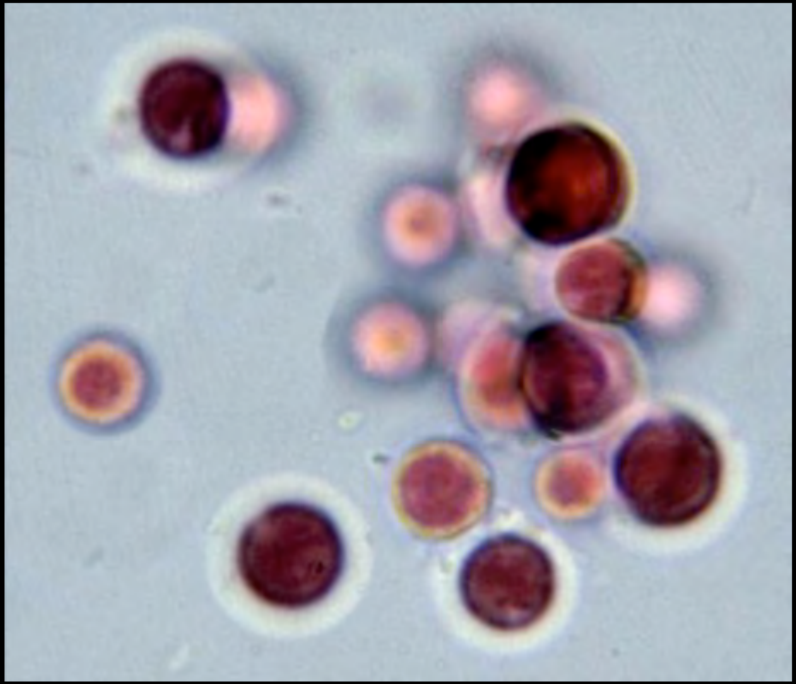


Suborder	Superfamily	Family	Subfamily	Species	Symbiont	Water depth range (m)
Miliolina	Soritacea	Peneroplidae		*Peneroplis planatus* *Peneroplis pertusus* *Spirolina arietina*	Rhodophyceans	0–60/70
				Laevipeneroplis proteus	Chlorophyceans	0–15
		Soritidae	Archaiasinae	*Cyclorbiculina compressa* *Archaias angulatus*		
			Soritinae	*Sorites orbiculus* *Sorites variabilis* *Sorites marginalis* *Amphisorus hemprichii* *Marginopora vertebralis*	Dinophyceans	0–60/70
		Alveolinidae		*Borelis schlumbergeri* *Alveolinella quoyi*	Diatoms	2–70
Rotaliina	Asterigerinacea	Amphisteginidae		*Amphistegina lobifera* *Amphistegina lessonii* *Amphistegina bicirculata* *Amphistegina papillosa* *Amphistegina radiata*		0–130
	Nummulitacea	Nummulitidae		*Operculina ammonoides* *Heterostegina depressa* *Heterocyclina tuberculata* *Cycloclypeus carpenteri* *Nummulites cumingii*		0–130
	Rotaliacea	Calcarinidae		*Calcarina calcar* *Calcarina spengleri* *Baculogypsina sphaerulata*		0–30

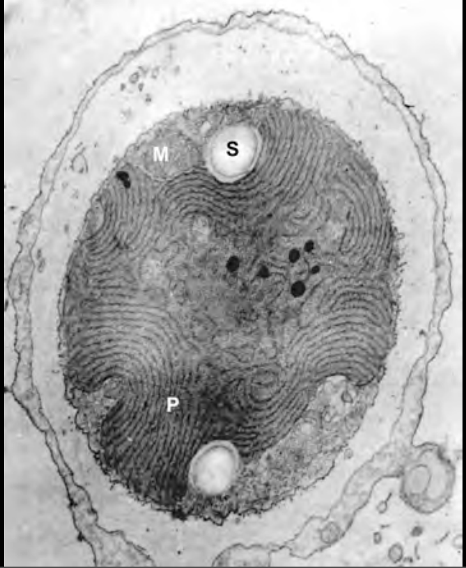
Murray (1991)

The symbiotic algae belong to several different taxa: Rhodophyceans, Chlorophyceans, Dinophyceans (zooxanthellae), Diatoms.

Rhodophyta (low profit on glycerol)

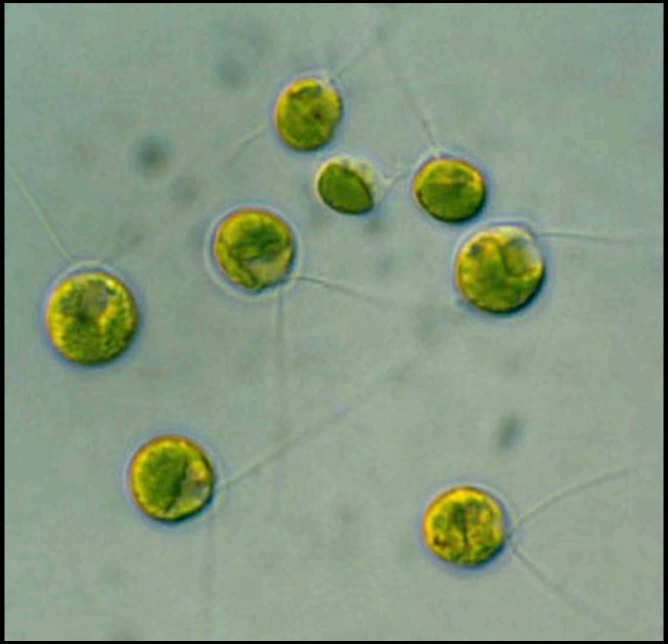


Porphyridium

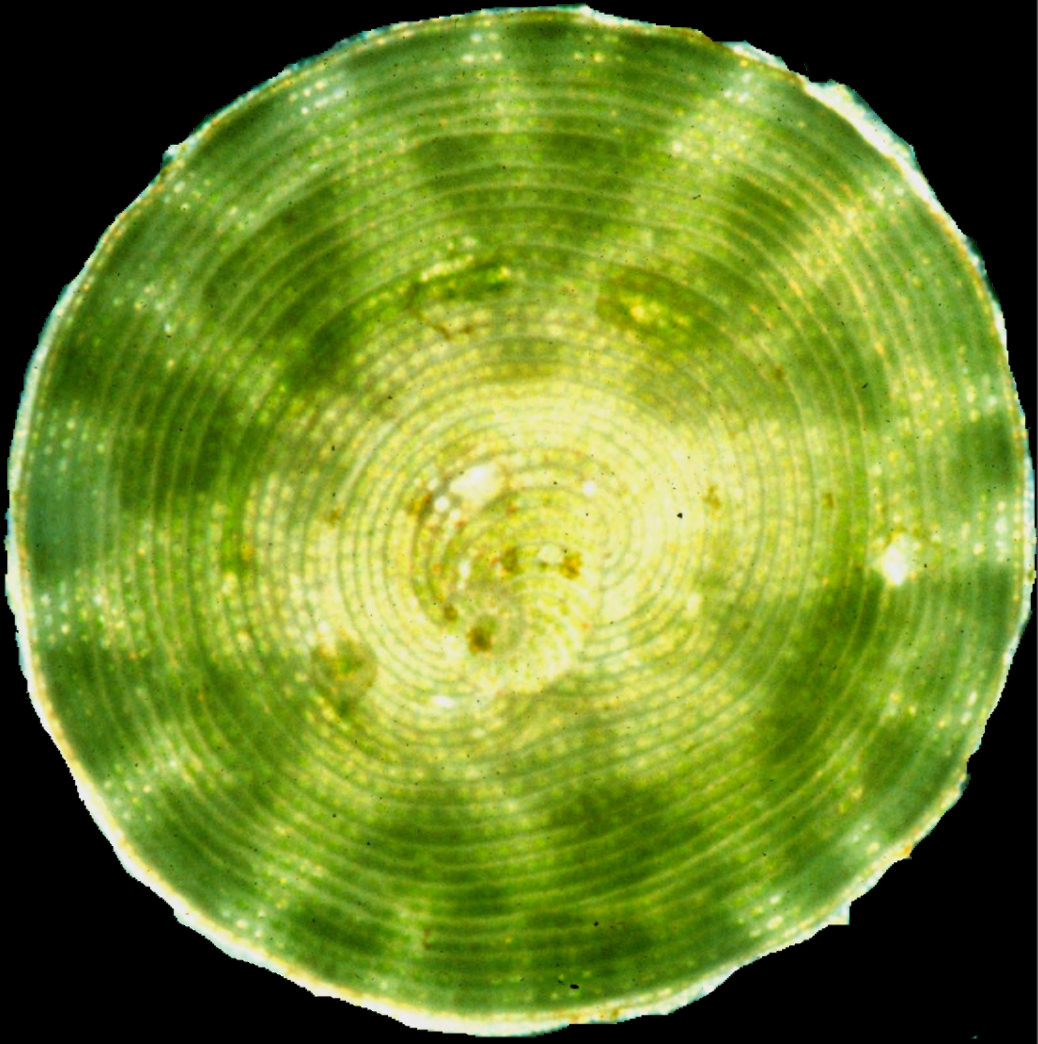


Dendritina

Chlorophyta (mean profit of glycerol and lipids)

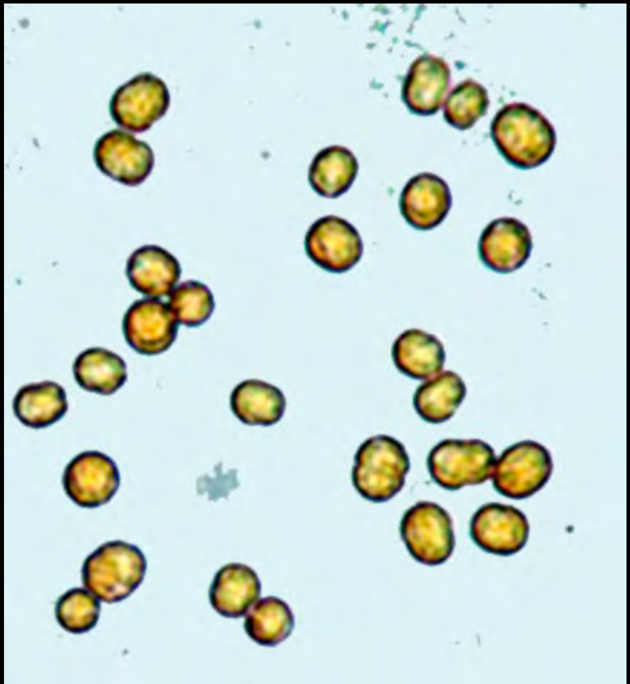


Chlamydomonas

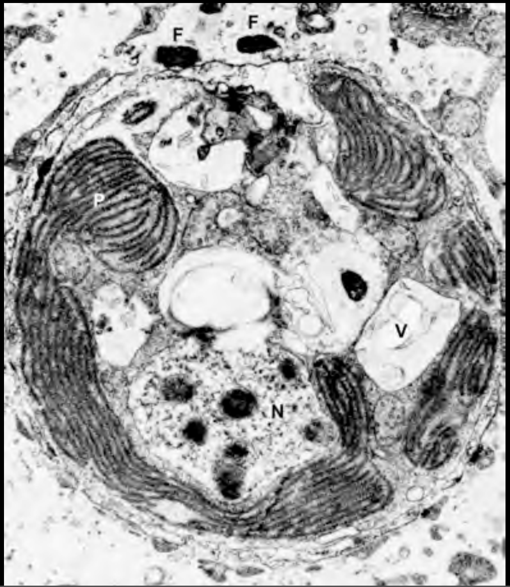


Parasorites

Zooxanthellae (high profit of glycerol and lipids)



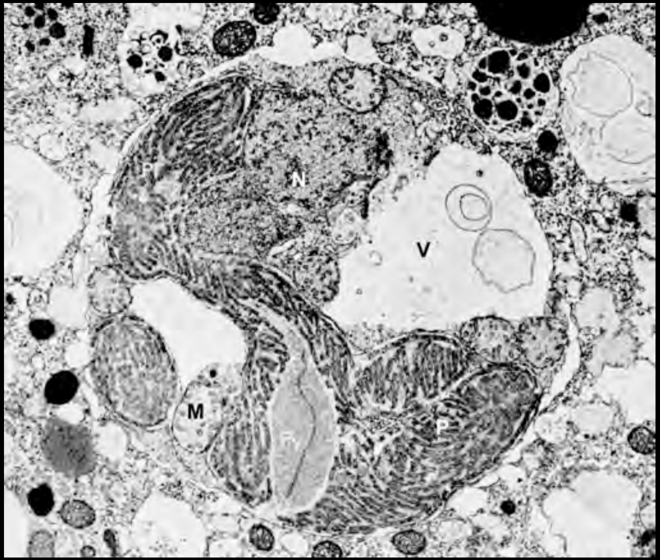
Symbiodinium



Amphisorus

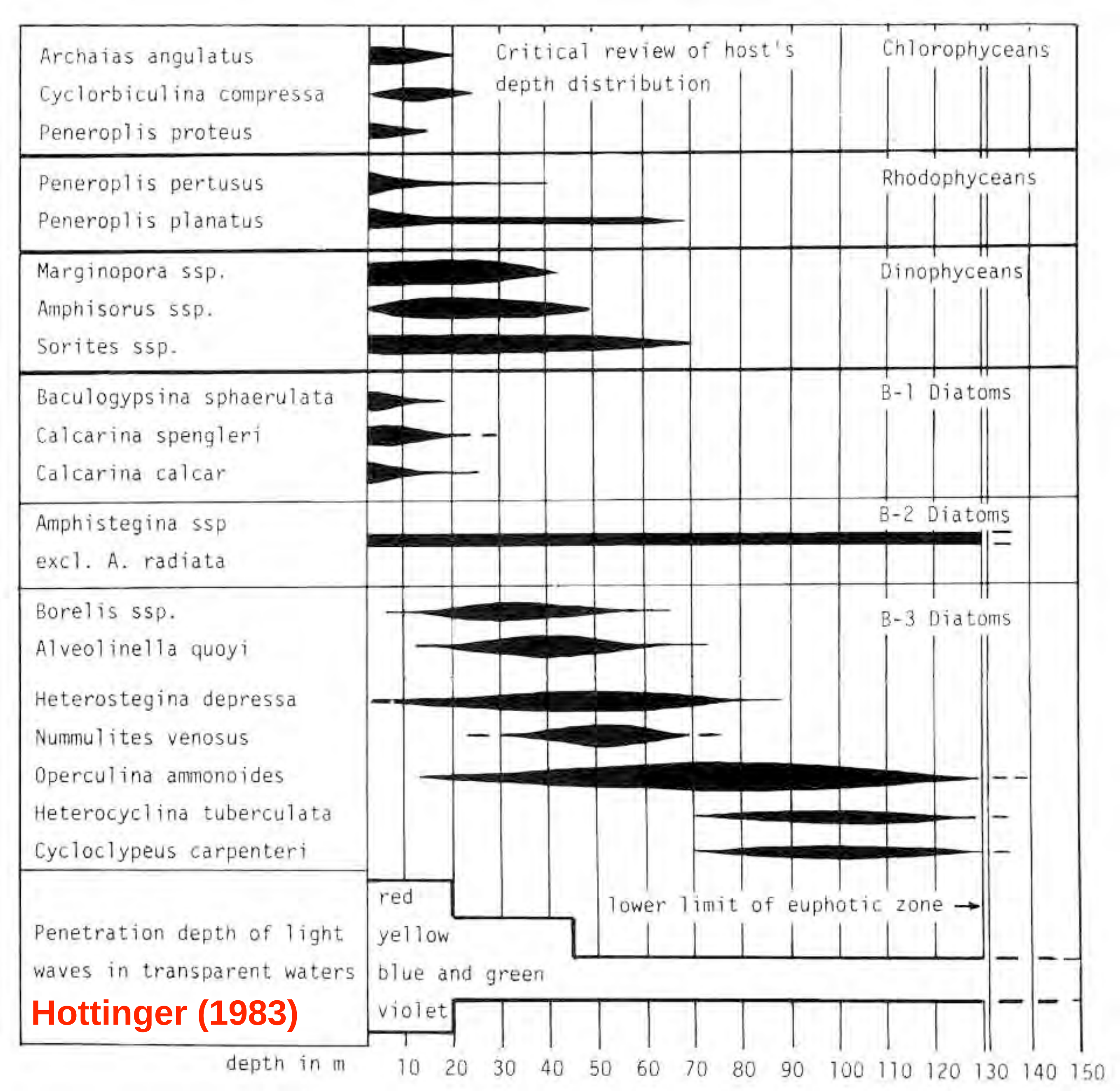
Diatoms (extreme profit of glycerol and lipids)

Thalassionema



Planostegina

Symbiosis in LF



Hottinger (1983)

Hosting photosynthetic algae constrains LF to live inside the photic zone.

Note the depth distributions are tightly connected with the characteristics of symbiotic algae.

Symbiosis in LF

Wall Material

Symbiosis in LF

Wall Material

- Small high-magnesium calcite needles (porcelaneous)

Symbiosis in LF

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Symbiosis in LF

Wall Material

- Small high-magnesium calcite needles (porcelaneous)
- Small low-magnesium calcite plate-like crystallites (hyaline)

Symbiosis in LF

Wall Material

- Small high-magnesium calcite needles (porcelaneous)
- Small low-magnesium calcite plate-like crystallites (hyaline)

Symbiosis in LF

Wall Material

- Small high-magnesium calcite needles (porcelaneous)
- Small low-magnesium calcite plate-like crystallites (hyaline)
- Agglutinated particles fixed by secreted calcium carbonate crystals (only in fossil larger benthics)

Symbiosis in LF

Wall Material

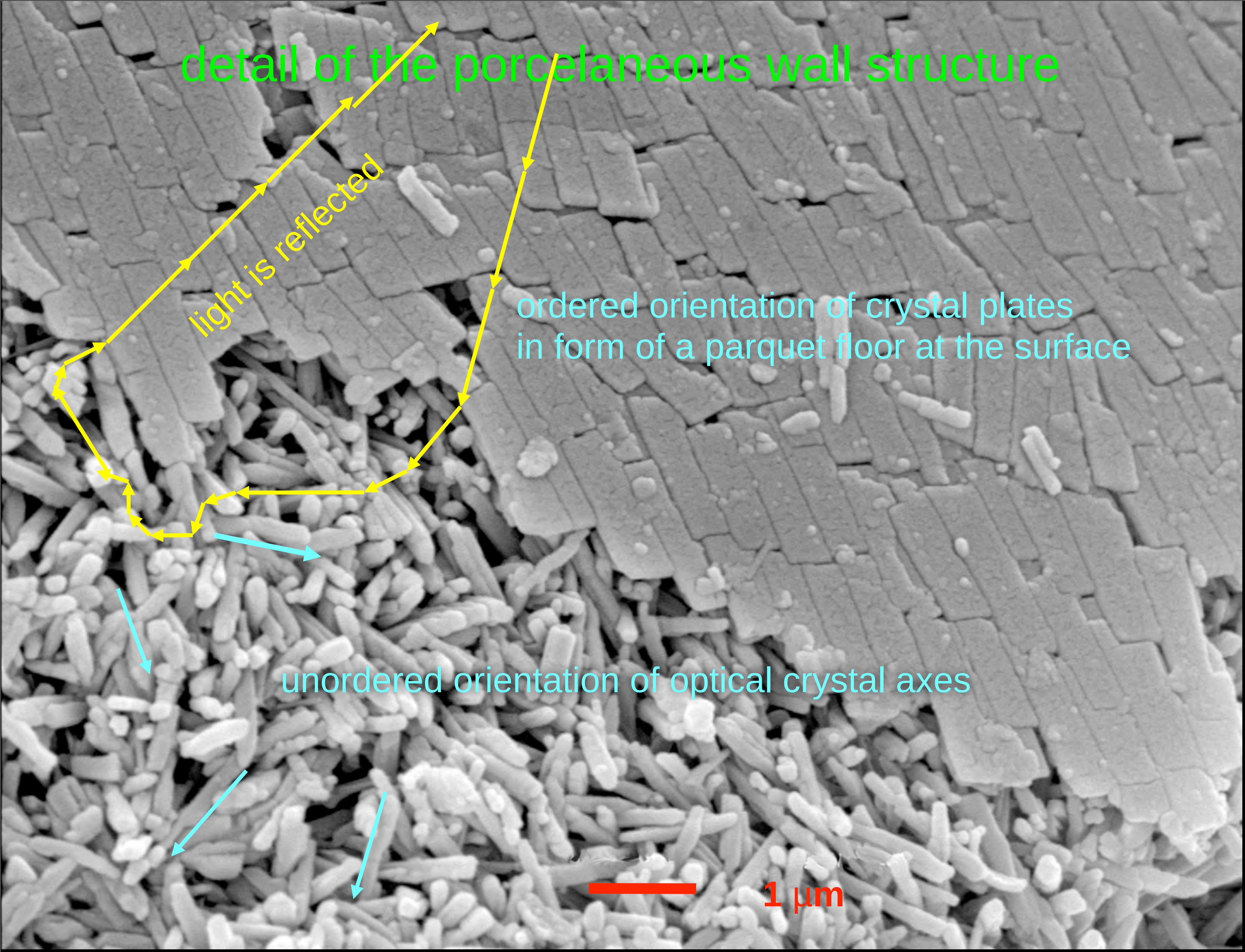
- Small high-magnesium calcite needles (porcelaneous)
- Small low-magnesium calcite plate-like crystallites (hyaline)
- Agglutinated particles fixed by secreted calcium carbonate crystals (only in fossil larger benthics)

Symbiosis in LF

Wall Material

- Small high-magnesium calcite needles (porcelaneous)
- Small low-magnesium calcite plate-like crystallites (hyaline)
- Agglutinated particles fixed by secreted calcium carbonate crystals (only in fossil larger benthics)
- † Small spheric calcite crystals (Fusulinida)

detail of the porcelaneous wall structure

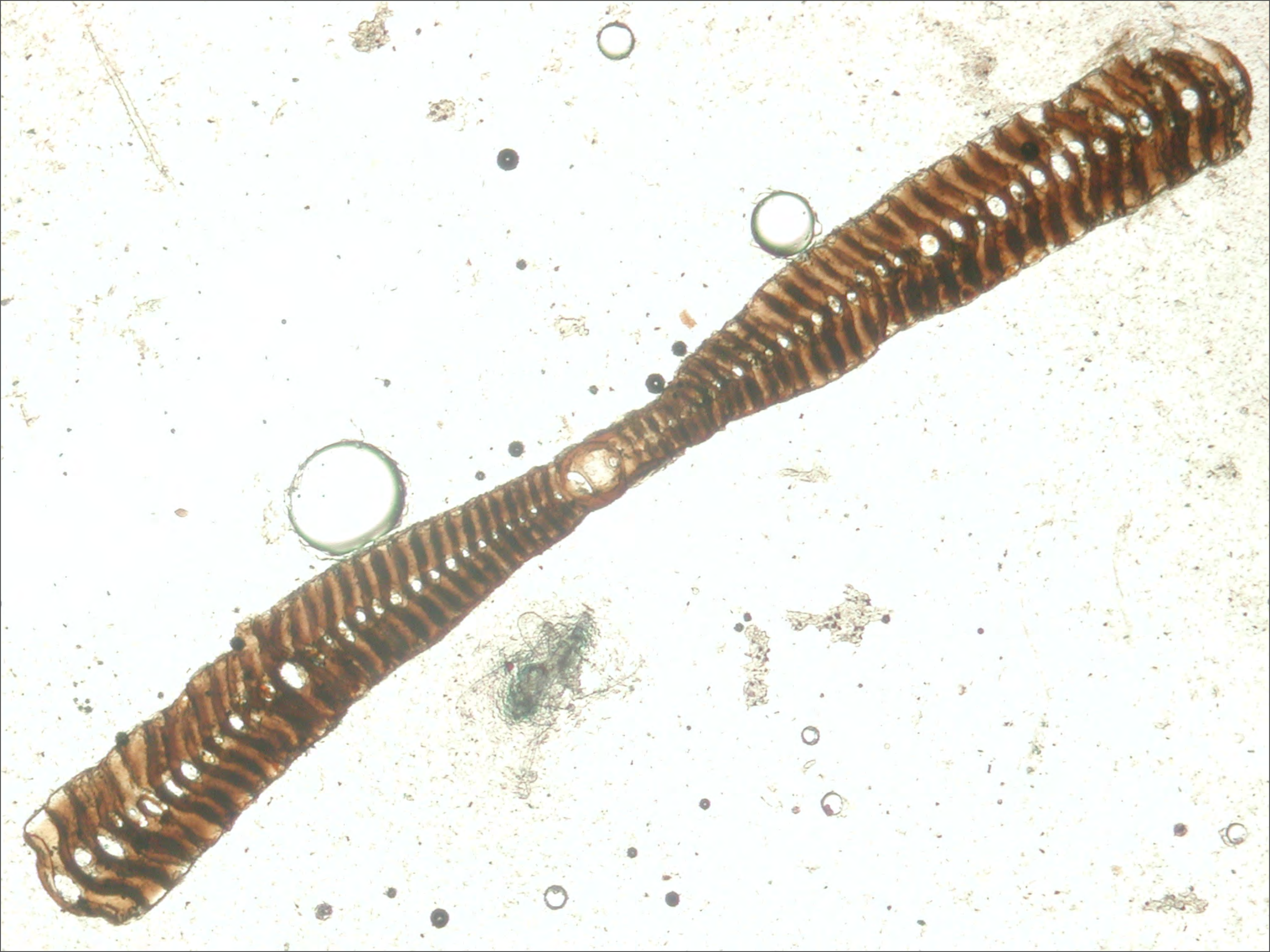


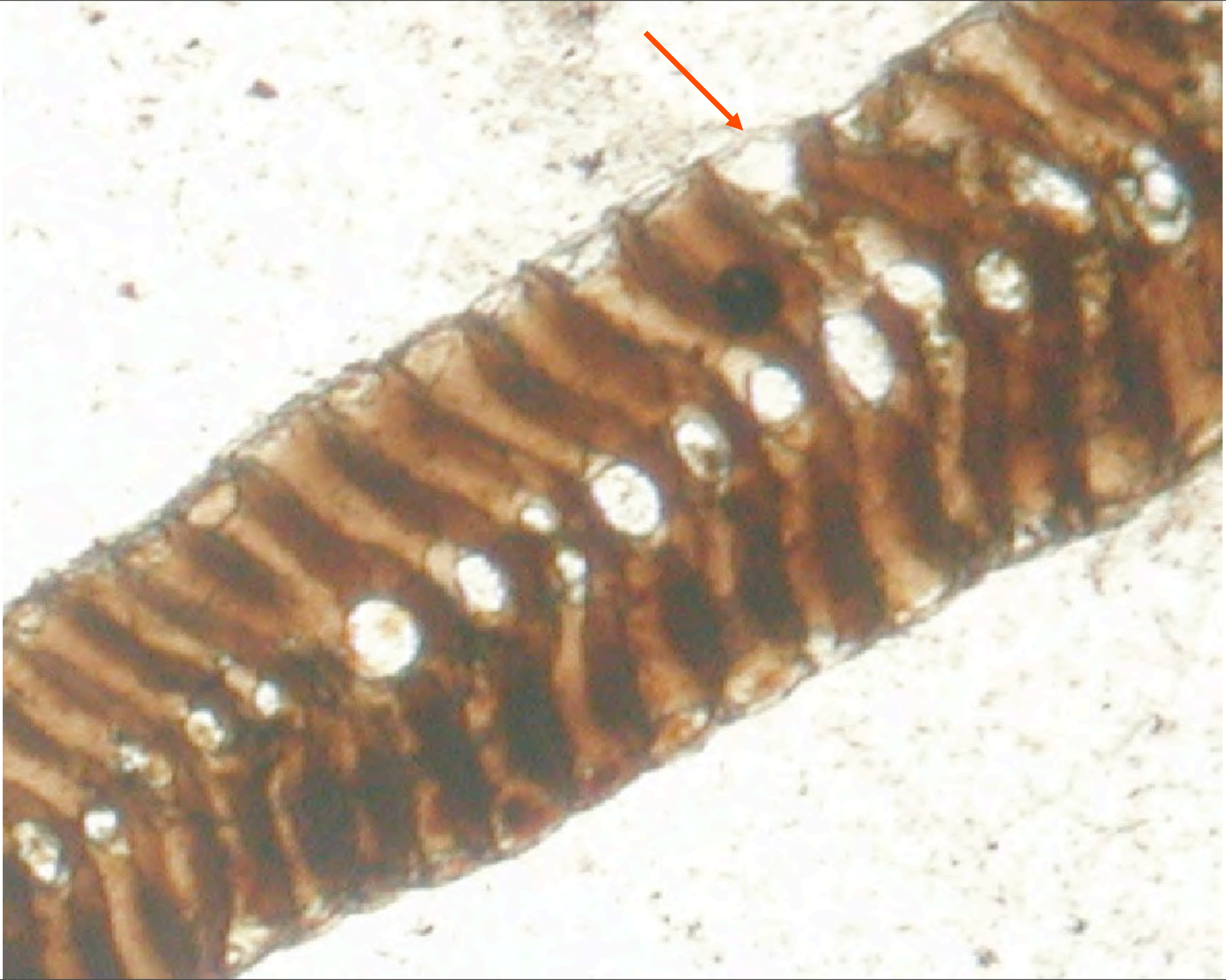
light is reflected

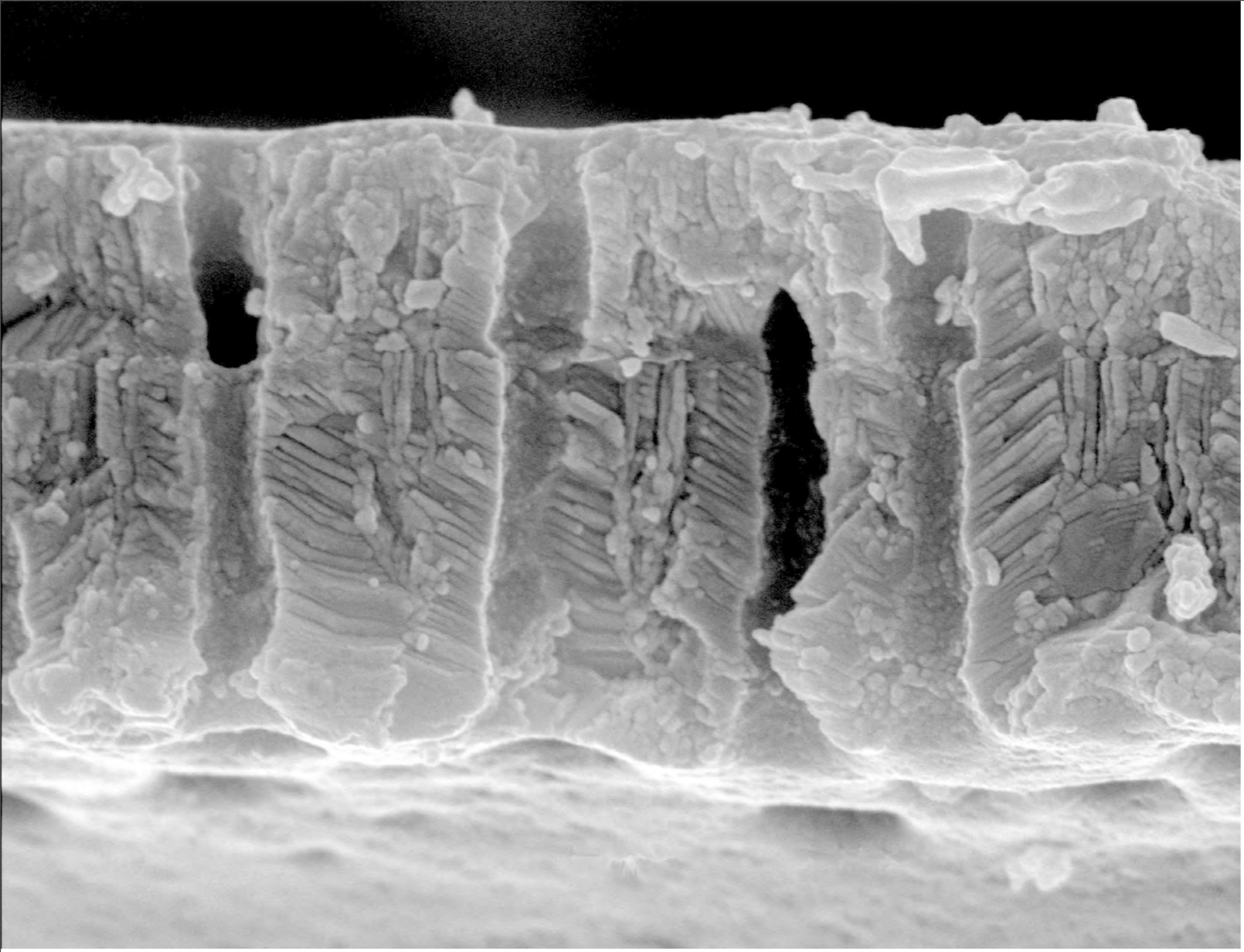
ordered orientation of crystal plates
in form of a parquet floor at the surface

unordered orientation of optical crystal axes

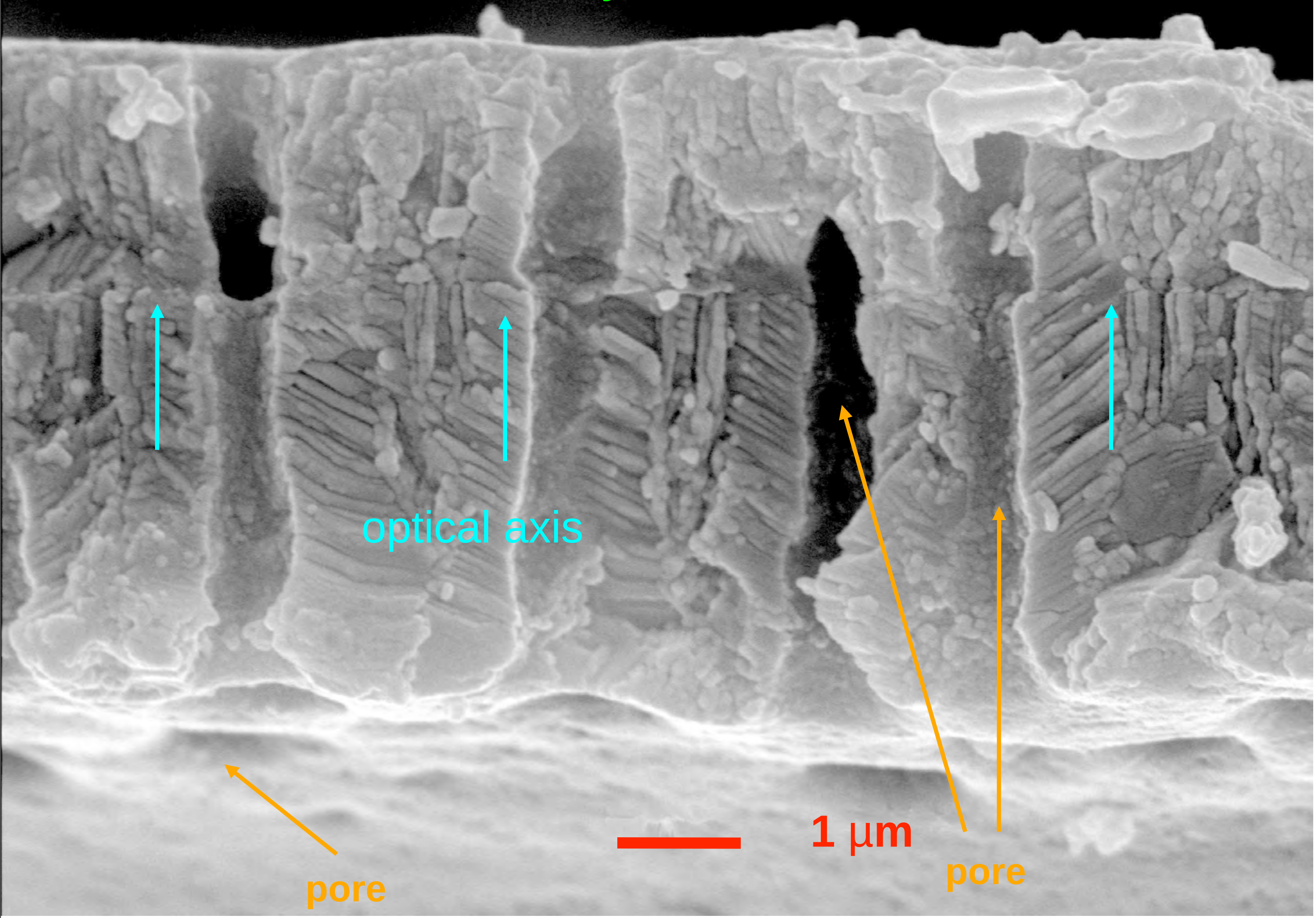
Parasorites orbitolitoides



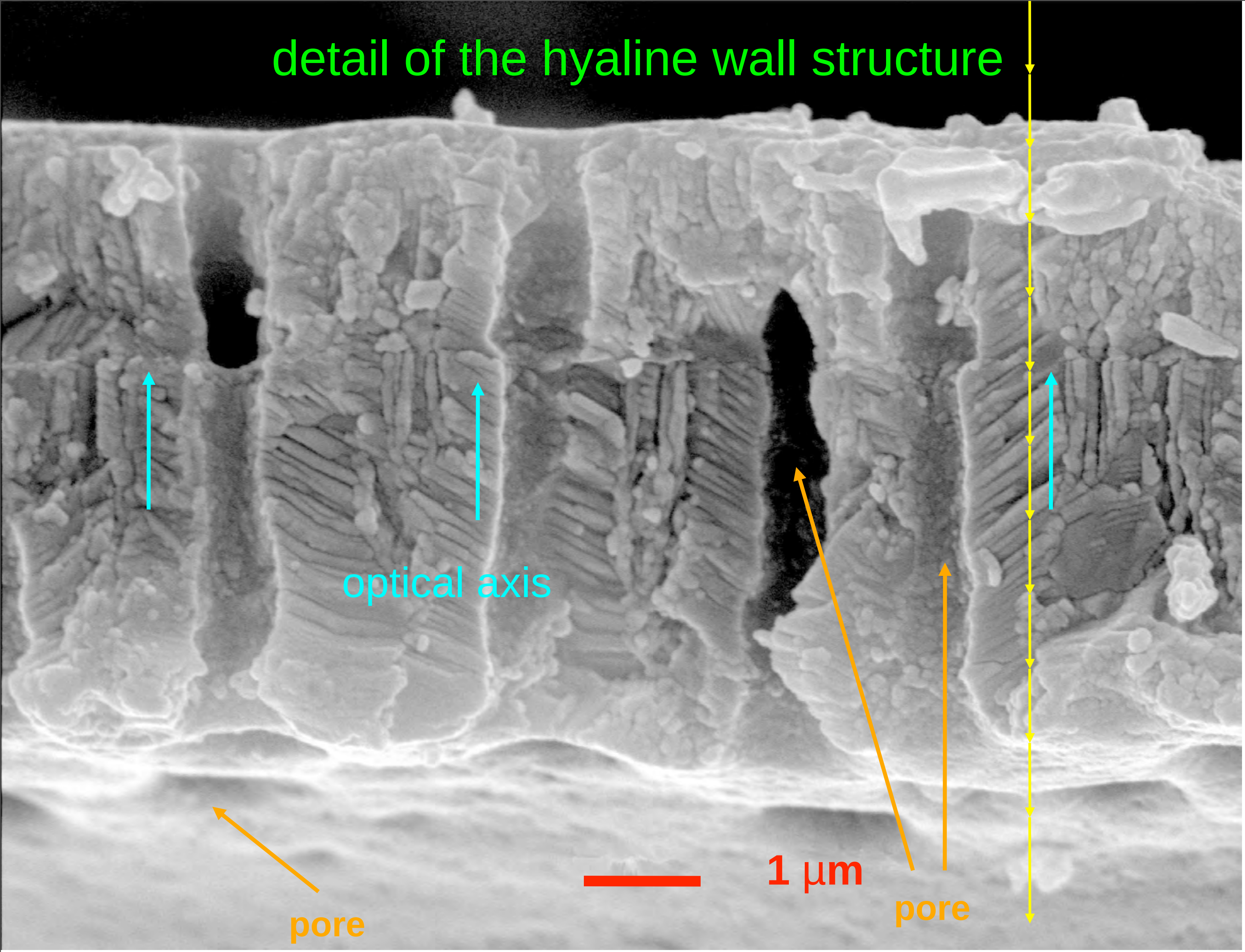




detail of the hyaline wall structure

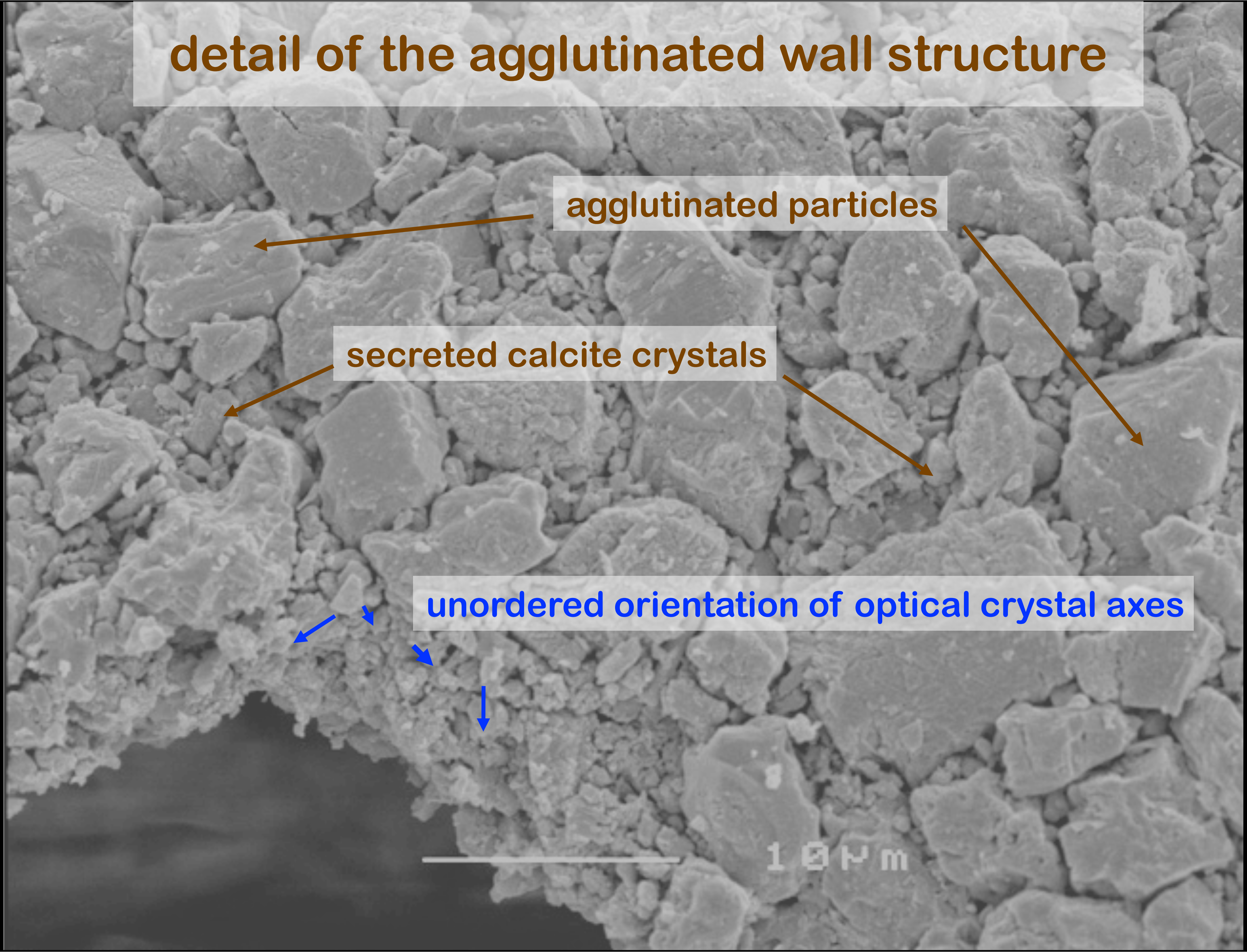


detail of the hyaline wall structure



Palaeonummulites venosus

detail of the agglutinated wall structure



agglutinated particles

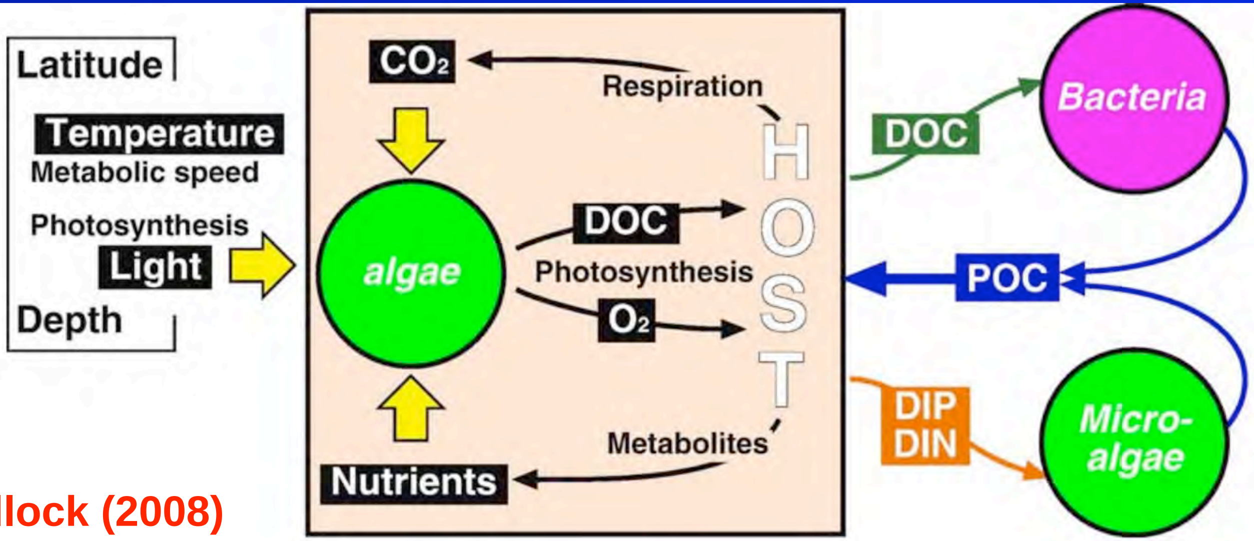
secreted calcite crystals

unordered orientation of optical crystal axes

Symbiosis in LF

The symbiosis provides at least two major advantages to the host:

1) it is a source of energy. This could account for the large size attained by LF, as their growth is sustained by the optimization of food supply and waste recycling.



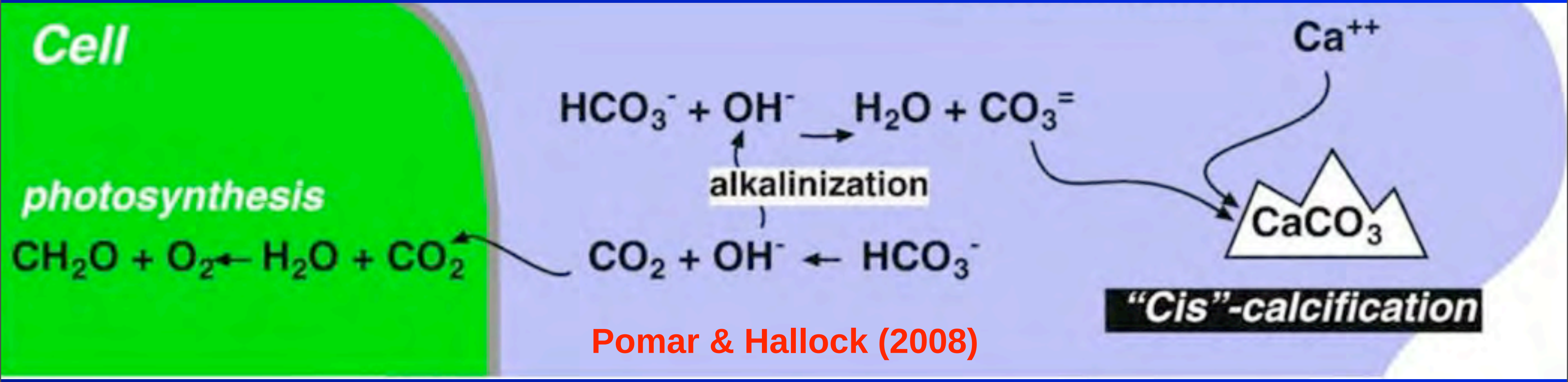
Pomar & Hallock (2008)

Fig. 3. Larger benthic foraminifers, with their symbiotic algae, rely on the efficiency of mixotrophy and on double external farming. In mixotrophy, the host provides respiratory CO_2 and nutrient wastes (dissolved inorganic nitrogen and phosphorus) to the symbiont. The algae provide oxygen and organic carbon (DOC) to the host, which provides energy for respiration and calcification as well as polysaccharides used in the organic matrix of the shell. In the external double farming, excess photosynthates (DOC) are used to farm bacteria and excess nutrient wastes to farm microalgae, on which the foraminifer can feed.

Symbiosis in LF

2) it enhances the calcium carbonate production. This is necessary to build the large, complex tests of LF. Two mechanisms could be responsible for the $CaCO_3$ precipitation:

a) "Cis"-calcification, results from photosynthetic alkalinization of the water during net carbon uptake.

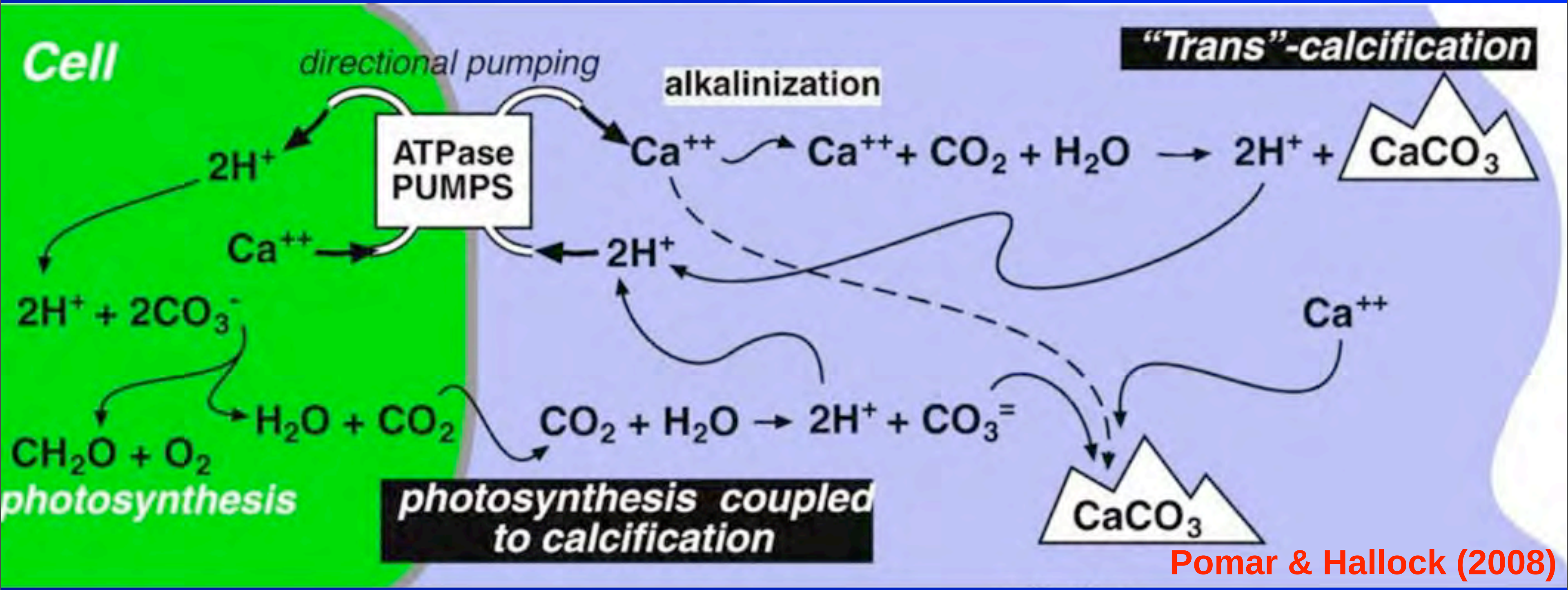


Pomar & Hallock (2008)

As result of CO_2 uptake, CO_3^{2-} and OH^- concentrate in the cell boundary layer. If the water is already supersaturated with respect to $CaCO_3$, precipitation may be biogeochemically induced.

Symbiosis in LF

b) “Trans”-calcification, with photosynthesis tightly coupled to calcification.

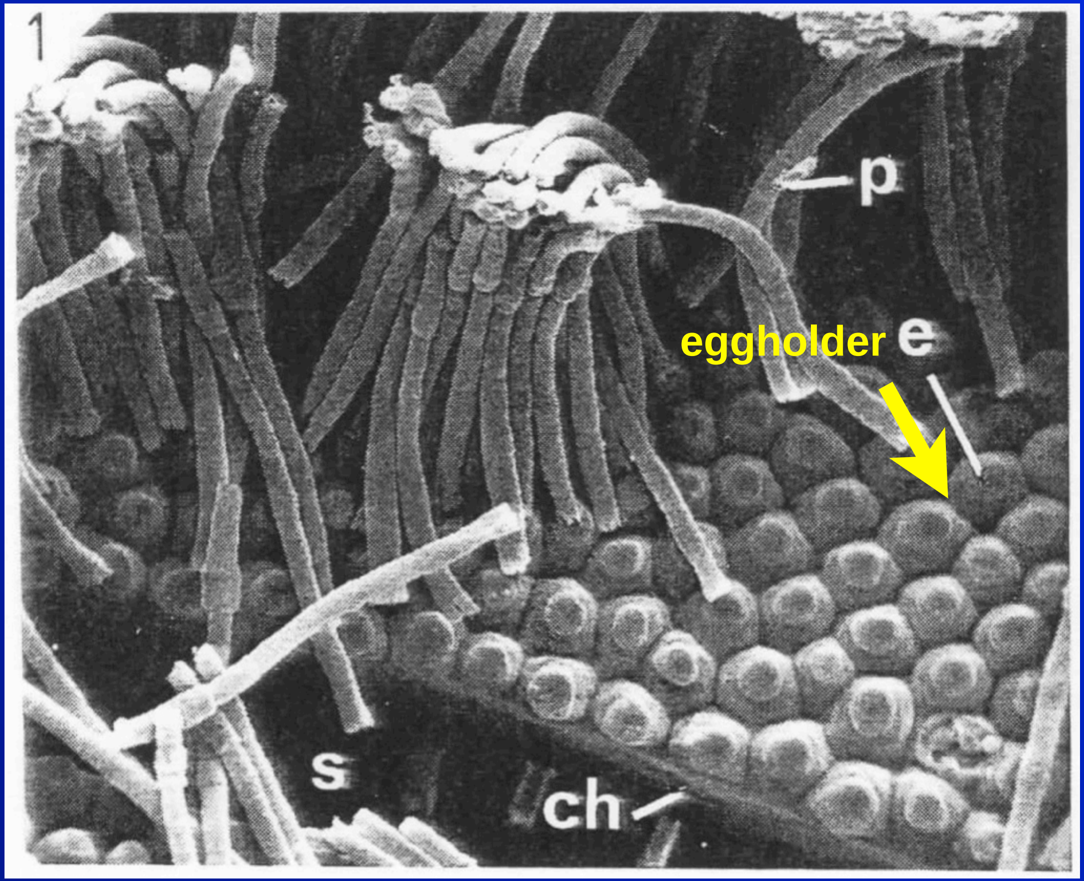


Pomar & Hallock (2008)

Photosynthesis is coupled to calcification through Ca^{++}-out/$2H^+$-in (ATPase pumps). Via this mechanism, each $2H^+$ uptake facilitates the conversion of $2HCO_3^-$ to $2CO_2$ inside of the cell ($2HCO_3 + 2H^+ \rightarrow 2CO_2 + 2H_2O$). One of these CO_2 molecules can be used for photosynthesis, whereas the other diffuses outside the cell.

Symbiosis in LF

Test structure and symbiosis: modern *Amphistegina*



Epoxy resin cast of cavities of the test in *Amphistegina papillosa* from the Gulf of Aqaba (Hottinger, 1997)

Lee & Hallock (1987)

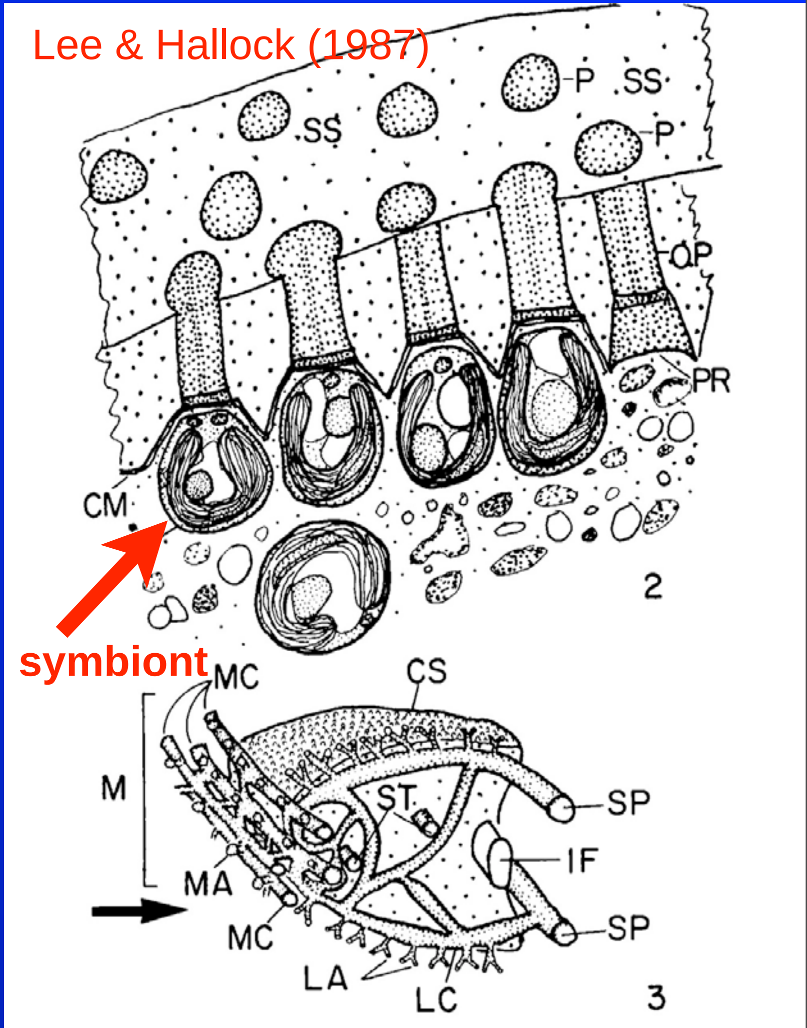


FIGURE 2. (2) Diagrammatic representation of the cortical region of *Amphistegina lobifer*
showing outer shell surface (SS), pores (P), organic pore lining (OP), cell membrane (CM
inner shell surface-pore rim (PR), symbiotic diatom (S). An SEM of shell architecture is show
in FIGURE 3(6). Based on TEMS by Koestler *et al.*[58] and Leutenegger.[13] Magnification ap
proximately 3200×. (3) Diagrammatic representation of canal system and chamber surface i
a single operculinid chamber showing marginal cord (M), intercameral foramen (IF), latera
apertures (LA), lateral canal (LC), lateral chamber surface (CS), marginal aperatures (MA
marginal canal (MC), septal chamber surface (SS), stolo (ST), spiral umbilical canal (SP
Redrawn from Hottinger and Dreher (1974) who based their interpretation of SEM observation
of casts made of the chamber spaces. A complete organism is shown in FIGURE 4. Imagin
looking at FIGURE 4(9) and dissolving away the shell. The chambers would look like FIGUR
2(3) when viewed from the direction of the arrow. Approximately 200×.

Symbiosis in LF

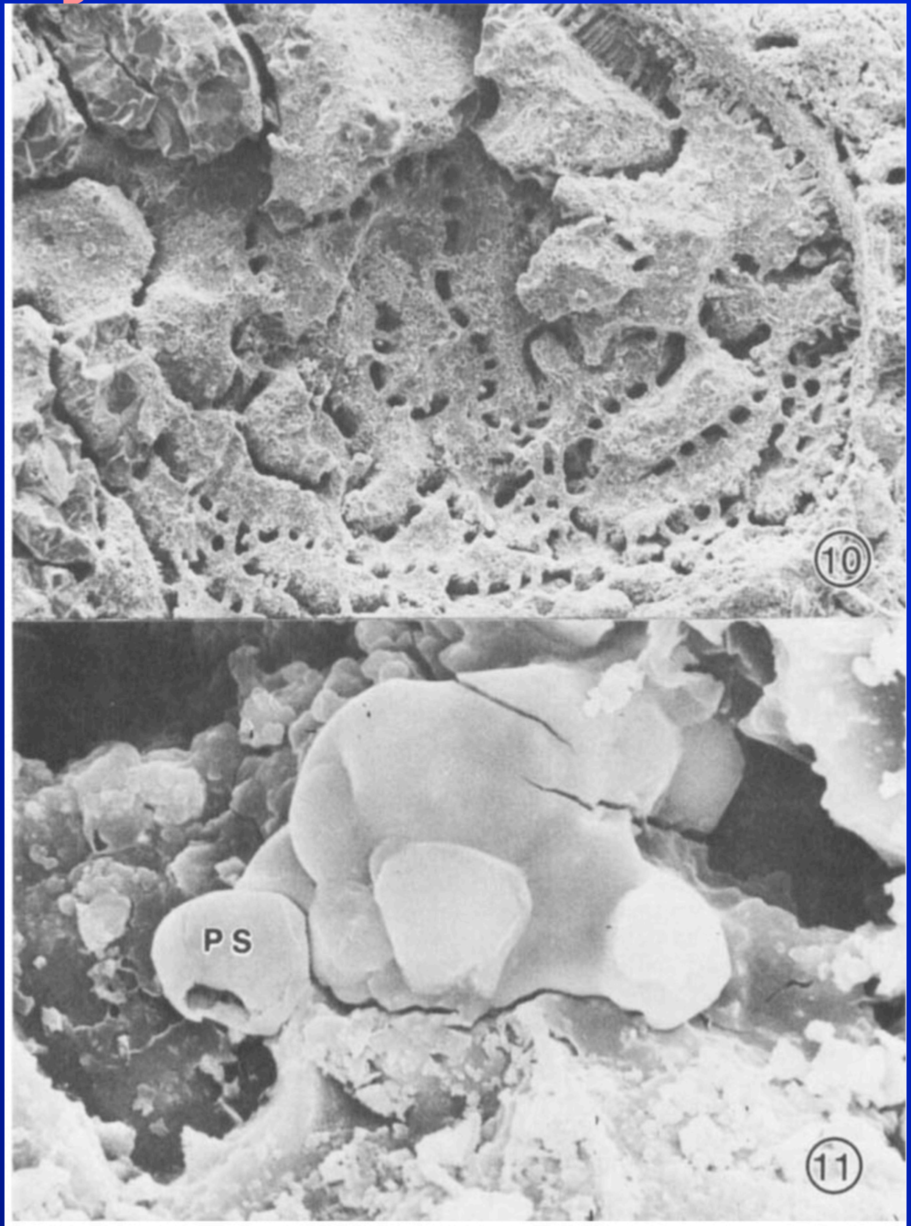
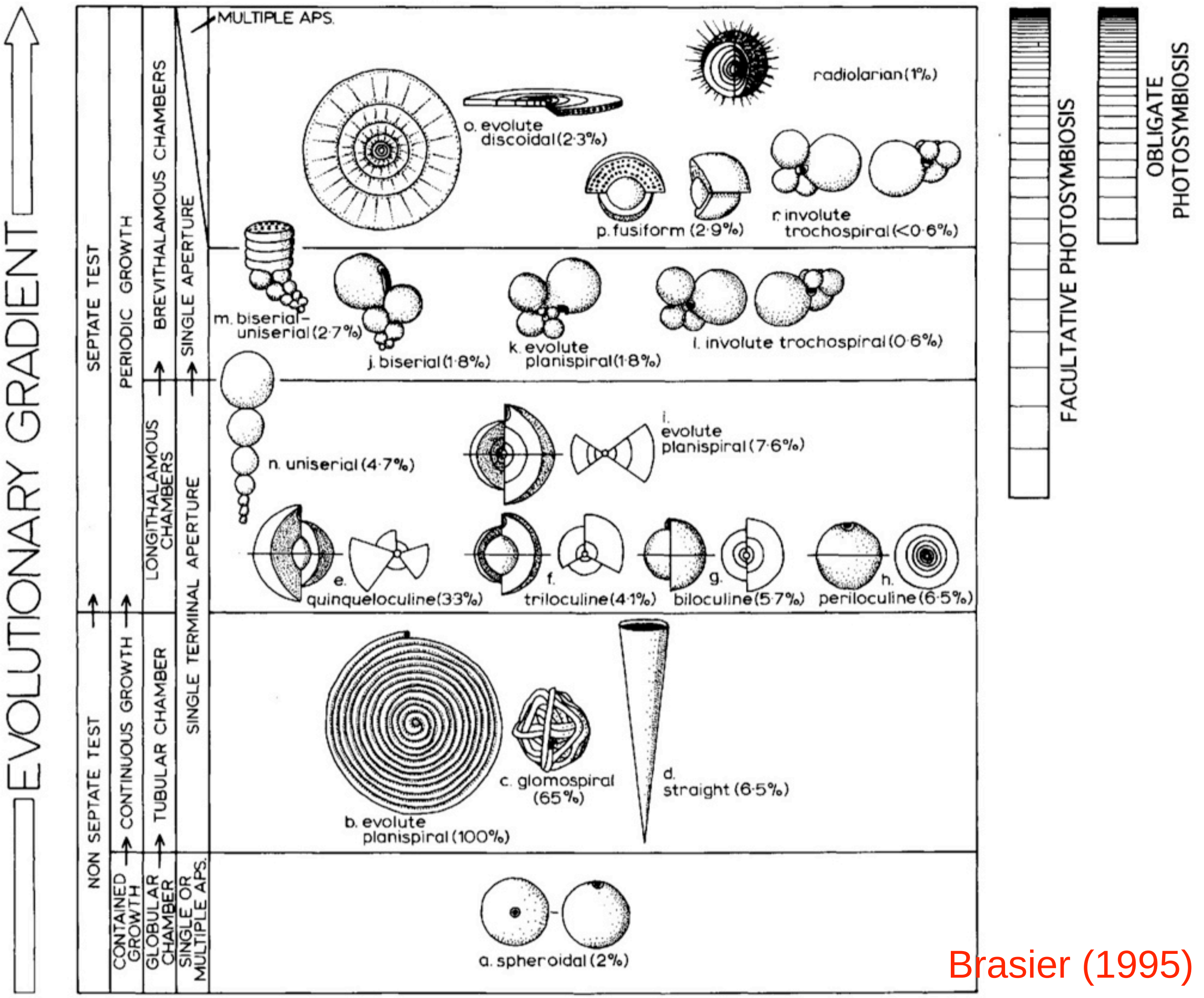


FIGURE 5. SEMs of a cut and etched *Pseudoschwagerina montanensis* from a sample of material used by Frenzel and Mundorff in their study of the Phosphoria formation of Montana.[28] (10) 85×. (11) Higher magnification (5000×) of the above showing putative symbiont (PS).

Test structure and symbiosis: extinct Fusulinida (*Pseudoschwagerina)*

Lee & Hallock (1987)

Symbiosis in LF

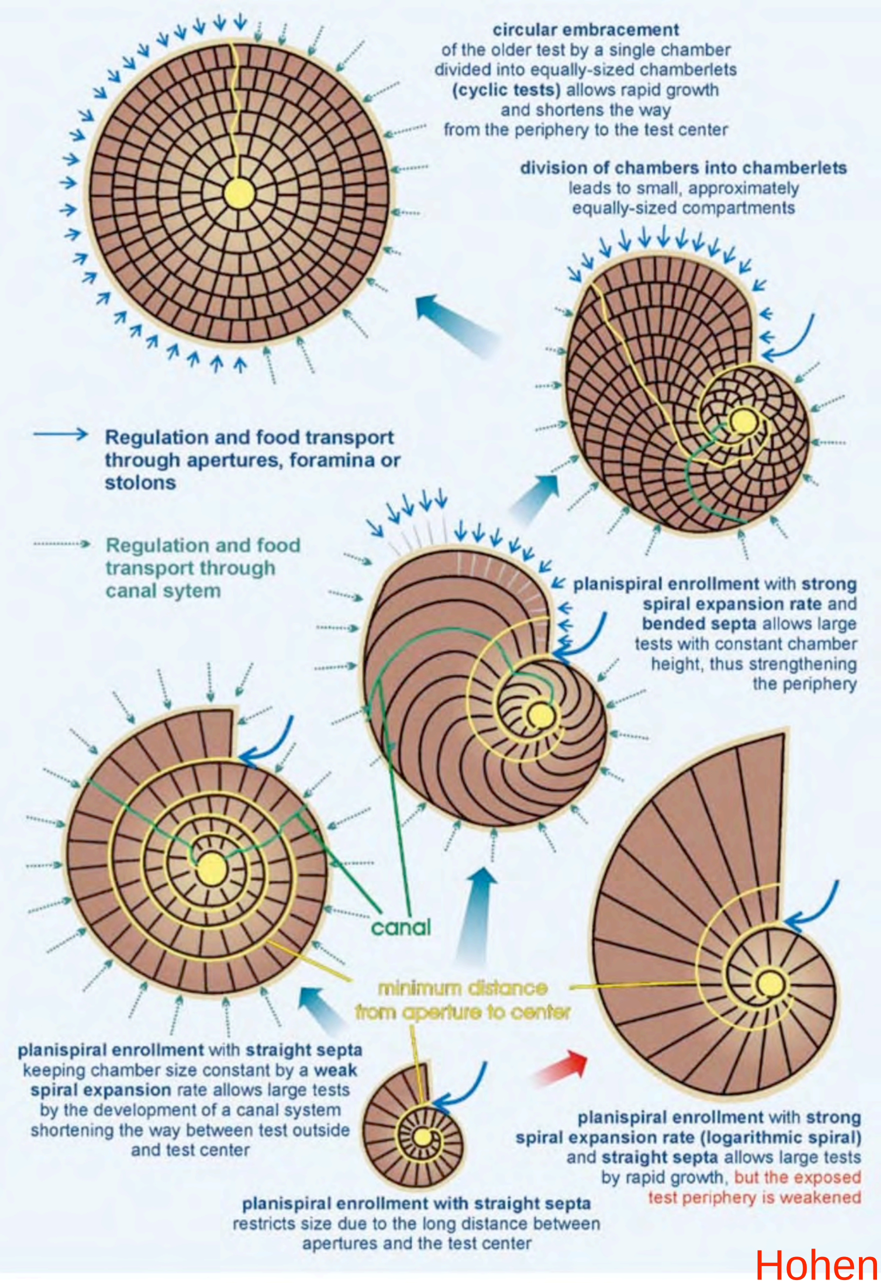


Brasier (1995)

Fig. 1. The evolutionary gradient in foraminiferid test architecture, from 'primitive' (below) to 'advanced' (above). Models of unit volume after Brasier (1982*a*) are used to compute the minimum line of communication (MinLOC), here given as a standardized percentage in brackets, relative to the evolute planispiral form 'b'. Forms with obligate photosymbiosis have relatively short lines of communication within the test. Adapted from Brasier (1986).

Evolution and K-strategy

Symbiosis in LF



circular embracement of the older test by a single chamber divided into equally-sized chamberlets **(cyclic tests)** allows rapid growth and shortens the way from the periphery to the test center

division of chambers into chamberlets leads to small, approximately equally-sized compartments

Regulation and food transport through apertures, foramina or stolons

Regulation and food transport through canal sytem

planispiral enrollment with **strong spiral expansion rate** and **bended septa** allows large tests with constant chamber height, thus strengthening the periphery

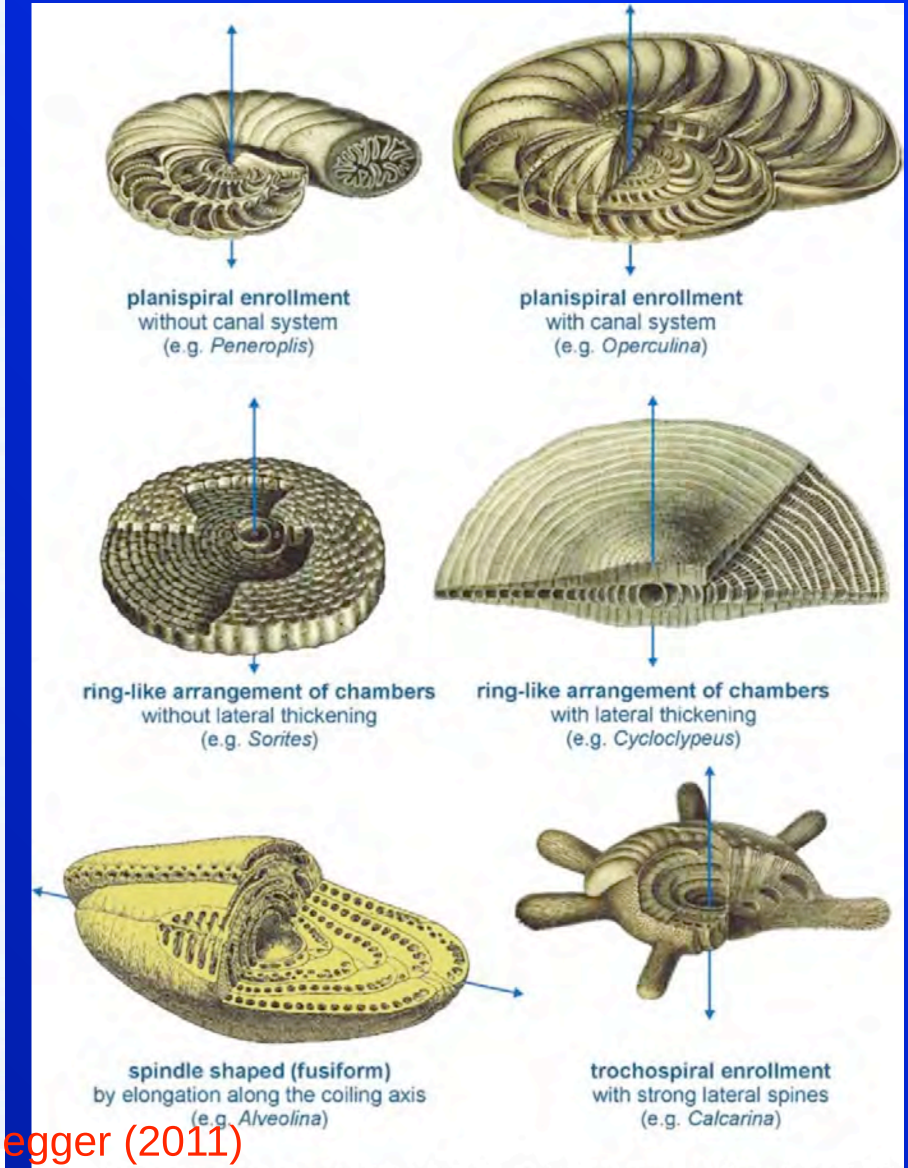
planispiral enrollment with **straight septa** keeping chamber size constant by a **weak spiral expansion** rate allows large tests by the development of a canal system shortening the way between test outside and test center

planispiral enrollment with straight septa restricts size due to the long distance between apertures and the test center

planispiral enrollment with **strong spiral expansion rate (logarithmic spiral)** and **straight septa** allows large tests by rapid growth, but the exposed test periphery is weakened

Figure 5. Different ways to construct large tests originating from an planispirally coiled test.

Test structure and symbiosis: going out straight



planispiral enrollment without canal system (e.g. *Peneroplis*)

planispiral enrollment with canal system (e.g. *Operculina*)

ring-like arrangement of chambers without lateral thickening (e.g. *Sorites*)

ring-like arrangement of chambers with lateral thickening (e.g. *Cycloclypeus*)

spindle shaped (fusiform) by elongation along the coiling axis (e.g. *Alveolina*)

trochospiral enrollment with strong lateral spines (e.g. *Calcarina*)

Hohenegger (2011)

Figure 6. Test constructions in modern larger foraminifera (drawings except *Alveolina* after Carpenter 1858, *Alveolina* modified after Reichel 1936).