

Recognising the full range of morphological variation in microspores produced by a single fossil plant species in dispersed assemblages; new observations from the Sleipner Formation (Middle Jurassic) of the North Sea.

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Morphological variability of reproductive cells produced by a single plant species.

- Numerous palaeobotanical studies have highlighted the wide morphological variation in microspores produced by a single parent species
- Not fully addressed by the palynological community

Main causes of morphological variation

- Late ontogenetic development prior to dispersal (e.g. fern spores)
- Other types of cell growth/development in spore-like cells with uncertain affinities
- Rupture of cell wall during germination/dehiscence

Ontogenetic Development Stages

Diez *et al* 2005 Examined spores from variably mature fern sporangia (Albian).

ODS1

Each contained a population of equally mature microspores, corresponding to the maturity of the sporangium.

ODS3

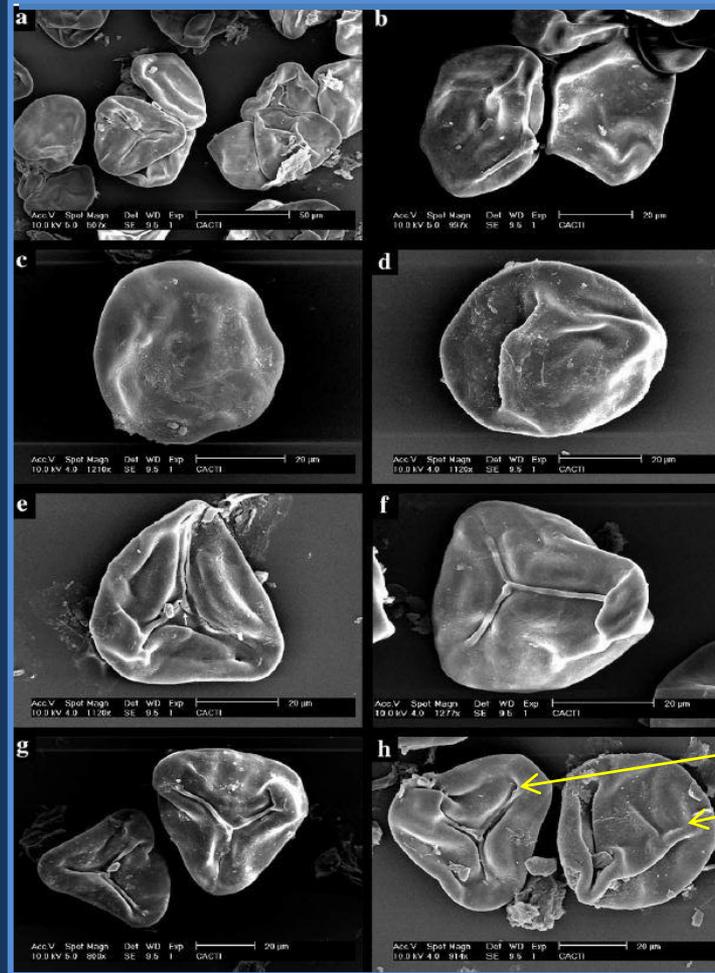
ODS1 = immature

ODS2 = maturing

ODS3 = mature = dispersal

ODS3

Diez *et al* 2005 Plate III



ODS1 = discoid, alete

ODS2

ODS2 – ODS3

ODS3 = triangular, trilete

ODS2

Applied here, but  only loose equivalents

Maturity of reproductive cells in dispersed assemblages

Generally assumed to be fully mature prior to dispersal.

In some terrestrial environments, large quantities of immature and maturing forms may be released by weathering and erosion processes.

If transportation from source is minimal, then microfloras recovered from these sediments can include substantial amounts of immature forms.

In addition, many cells are preserved still linked in life position to other reproductive cells or plant cell structures

Small numbers of immature & maturing microspores likely to occur in most assemblages. Proportional to distance offshore?



Sleipner Formation, Middle Jurassic NNS

○ = immature spores

Identifying the range of variability in reproductive cells from a single plant in dispersed assemblages

Evidence from

- Cells linked in life position
- Life cycle
- Internal structure

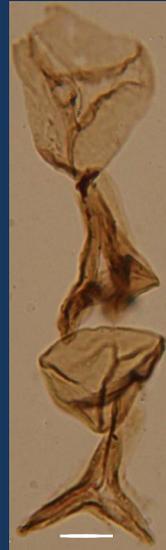
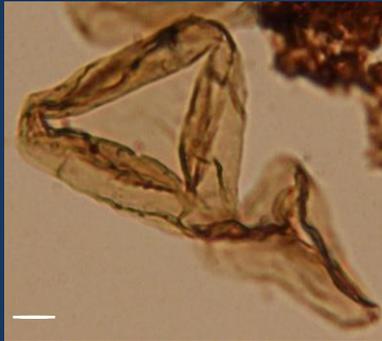
Cells linked in life position: - to other reproductive cells

linked to dissimilar cells - maturity?

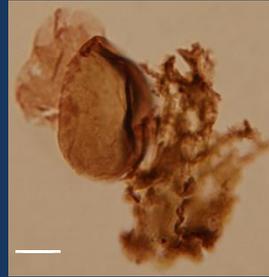
variety of linkage types

life cycles?

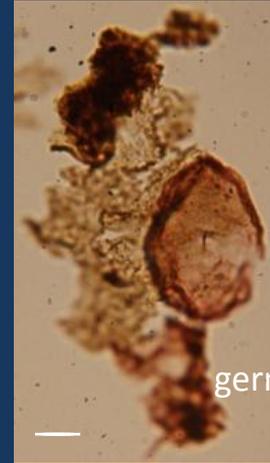
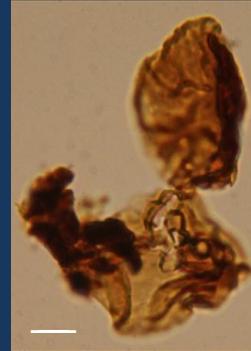
scale bars all 20 μ



■ cells linked to thalloid cell structures – diversity of life cycles

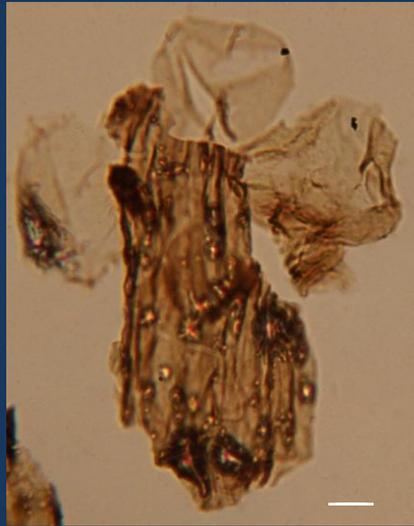


Todisporites

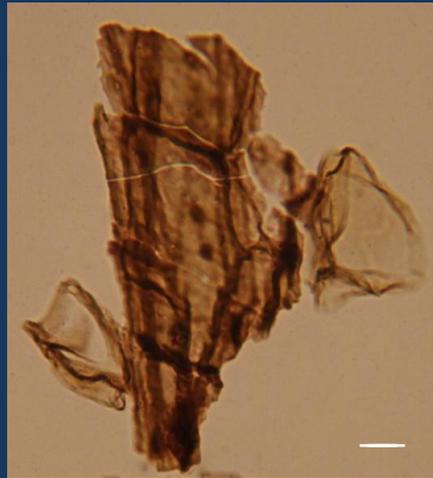


germinated?

single
cell



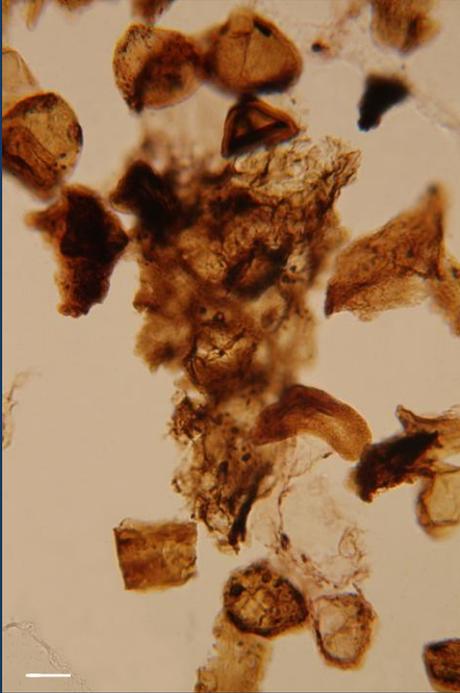
bar = 20 μ



multiple
cells -
?gemmae

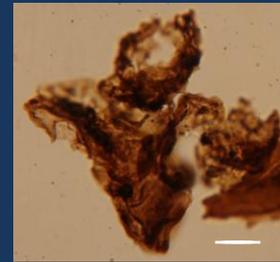
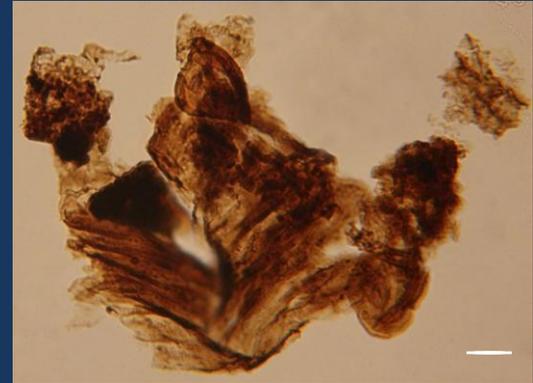
Remnant plant reproductive structures

- Fern sporangia with attached spores



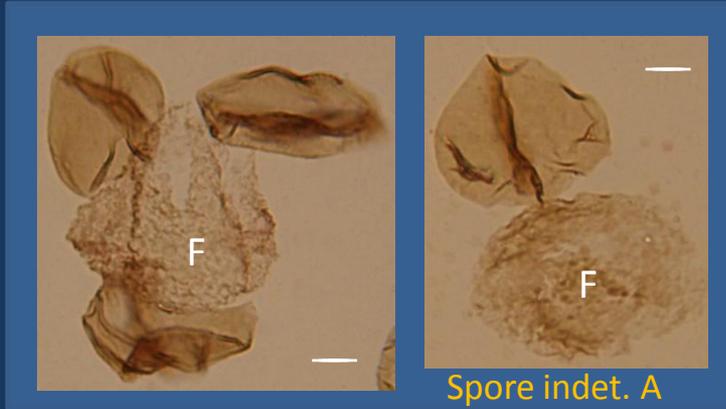
bar = 20 μ

- Unknown fruiting structures; possible liverwort with gemmae?

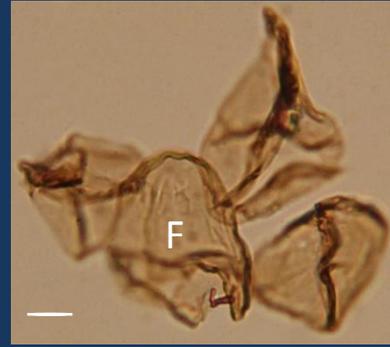


Different life-cycles

- Spore-like cells linked to “fruiting” cells



equally mature



equally mature

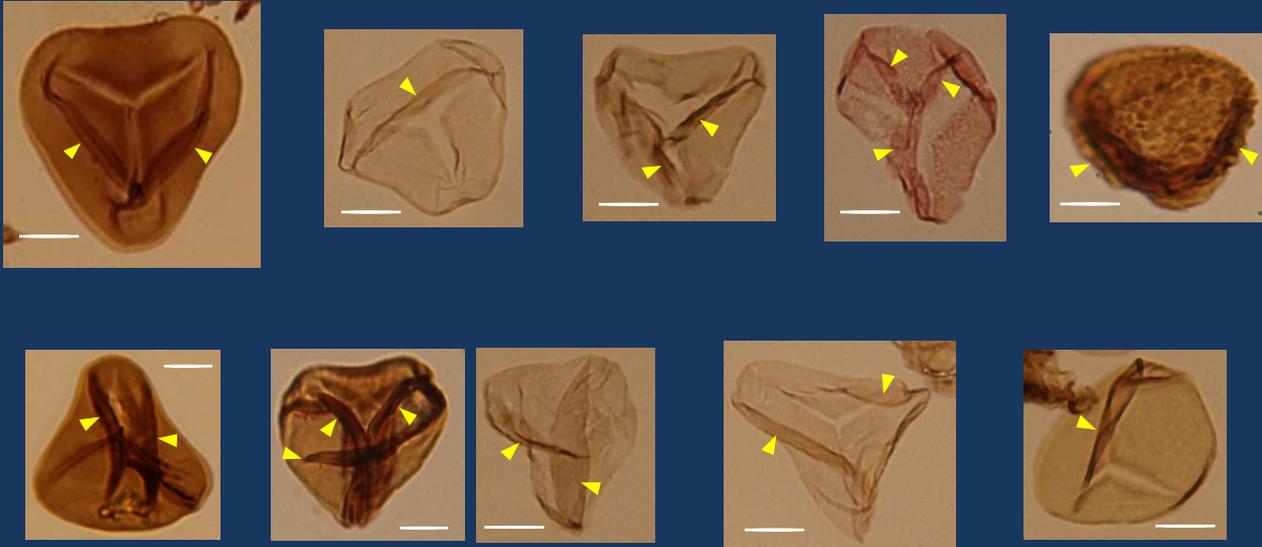


variably mature

- ❖ Linked cells give a direct match, but relatively rare to get such excellent preservation
- ❖ Interpretation of varied life-cycles requires botanical expertise

More widely applicable evidence →

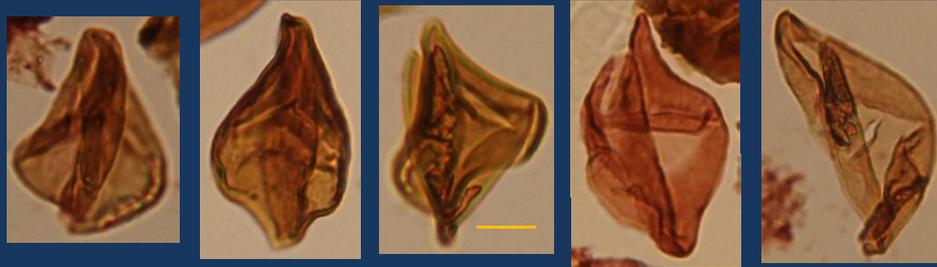
Evidence from internal structure



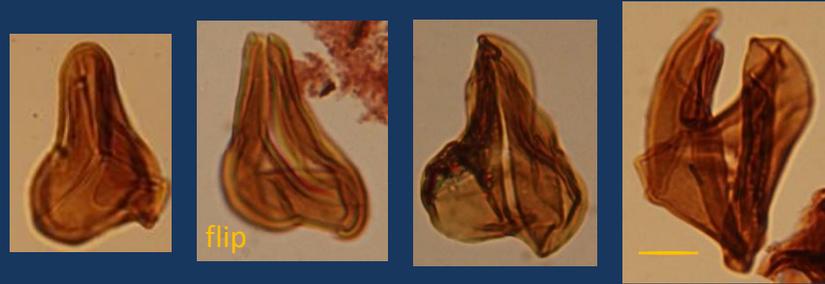
Normally treated as compressional folds

bar = 20 μ

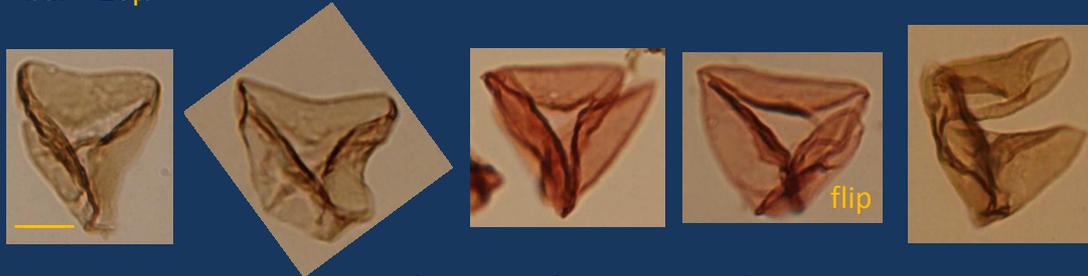
NOT
compression folds



Features are related to internal structure and development/growth of the ?spore (-like cell)



bar = 20μ



Also related to germination/dehiscence.

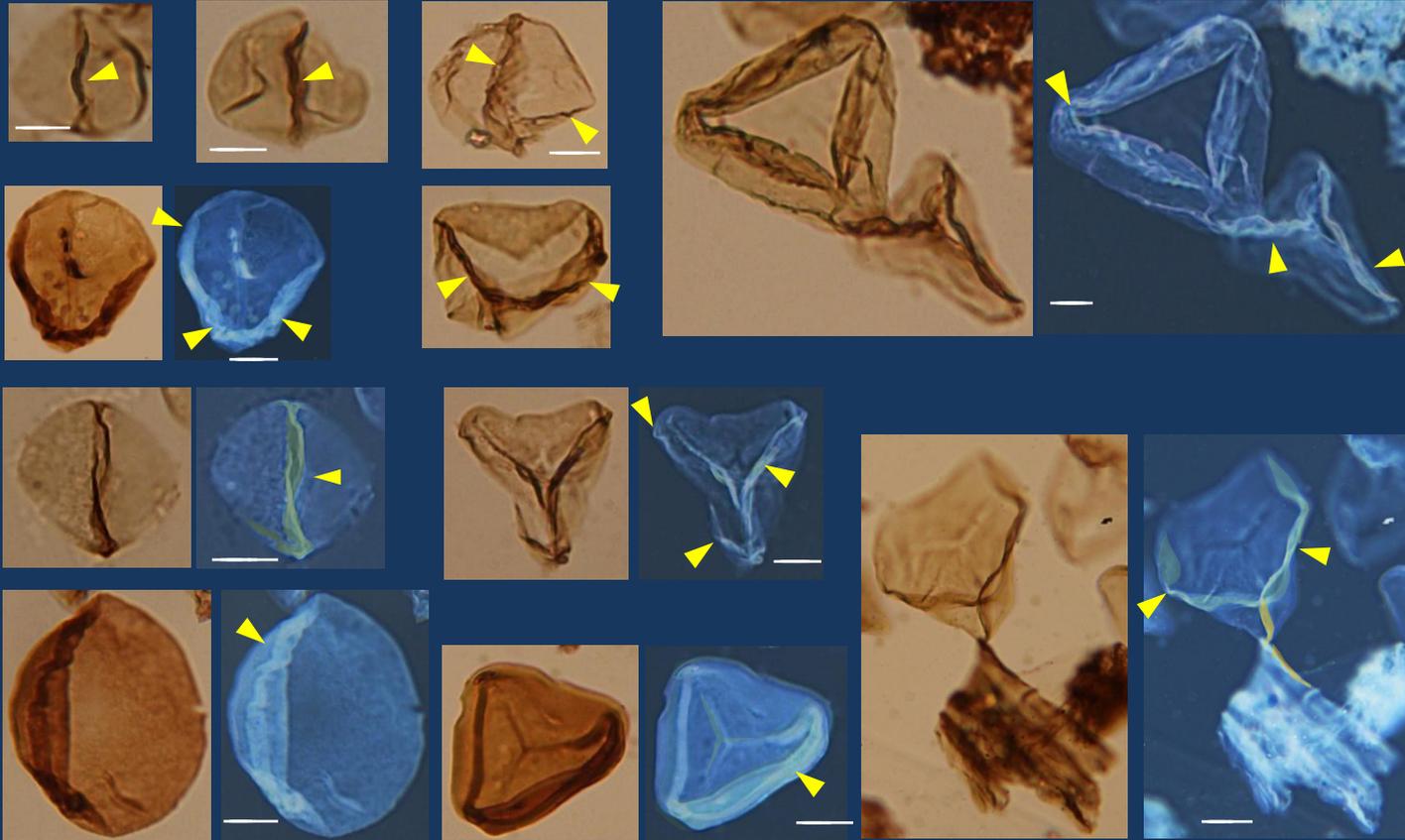
————— increasing maturity —————>

More evidence:-

The case against compressional folding

- Twisting axial growth
- **Scrolling**
- Continuous with external connective elements
- **Complexity of form**
- Consistency of form

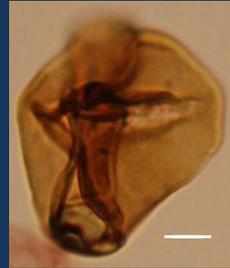
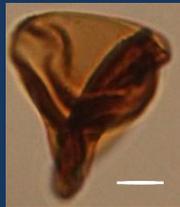
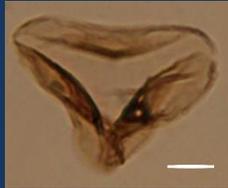
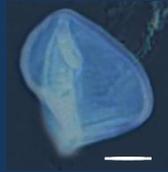
■ Twisting axial growth



bar = 20 μ

Individual elements twisted along direction of growth, or two elements around a common axis

■ Scrolling



bar = 20 μ

■ Continuous with external connective elements -

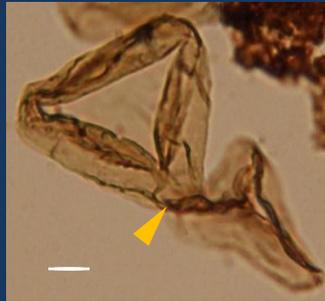
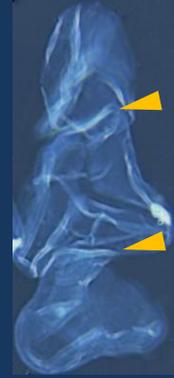
- which extend through the cell wall, connecting with similar features in adjacent reproductive cells.



bar = 20 μ



shared between 2 cells



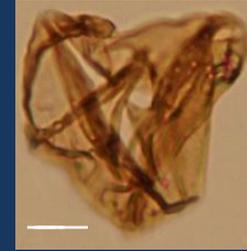
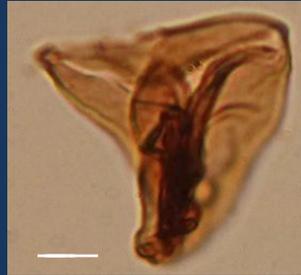
Axial structure extends into connective element at either pole



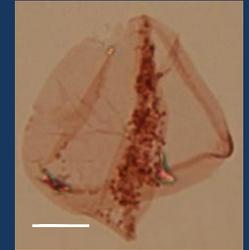
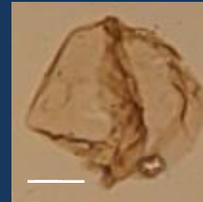
Adjacent cells often very dissimilar, - different maturity?

■ Complexity of form

overall structure



individual elements



Surface features of elements differ from cell wall

bar = 20μ



■ Consistency of form

Consistency in position, orientation and arrangement of elements



Primary morphological features, fundamental to cell development

bar = 20 μ

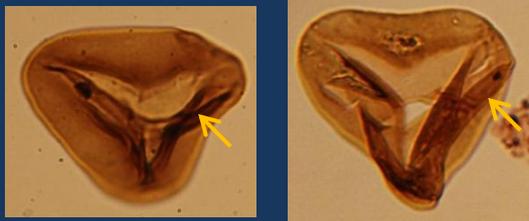
Interpreted as a single structure

Consistency of form

Other morphological features only form as the reproductive cell approaches maturity.

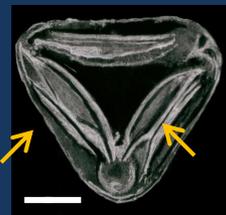
Parallel
secondary
elements

ODS 3



?*Cyathidites* sp. A

ODS 3



Cyathidites minor sensu Tahoun and Mohamed, (2014, Figure 3.11 (300°)).
Scale bar 10 μ , Jurassic.

ODS 3



Cyathidites mesozoicus
sensu Na et al. 2014 .

Distal secondary
elements

ODS 3



bar = 20 μ

Biretisporites sp. A

ODS 2



ODS 2



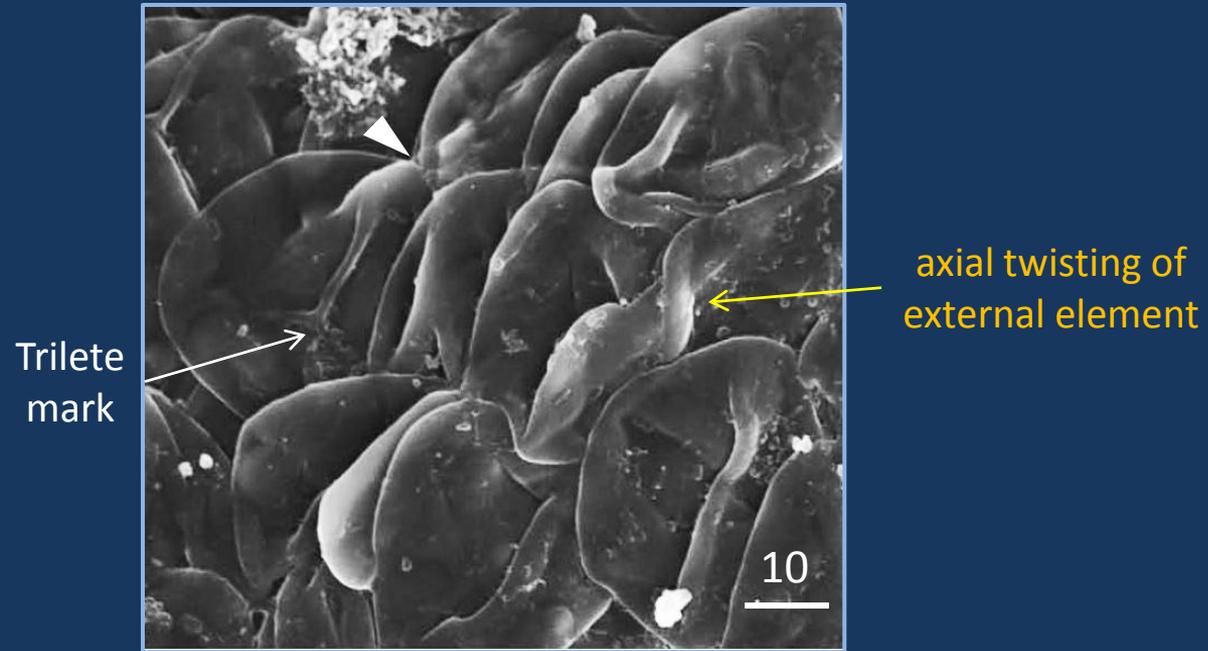
Verrucosisporites cf. *cheneyi*

ODS 3



Elements appear as positive features under SEM

Aligned into continuous features



Kvaček, J. and Dašková, J., 2010 Pl. 3, fig. 3

Microfolium

Enables orientation

Unique morphological characteristics = "habit"

Figure 1

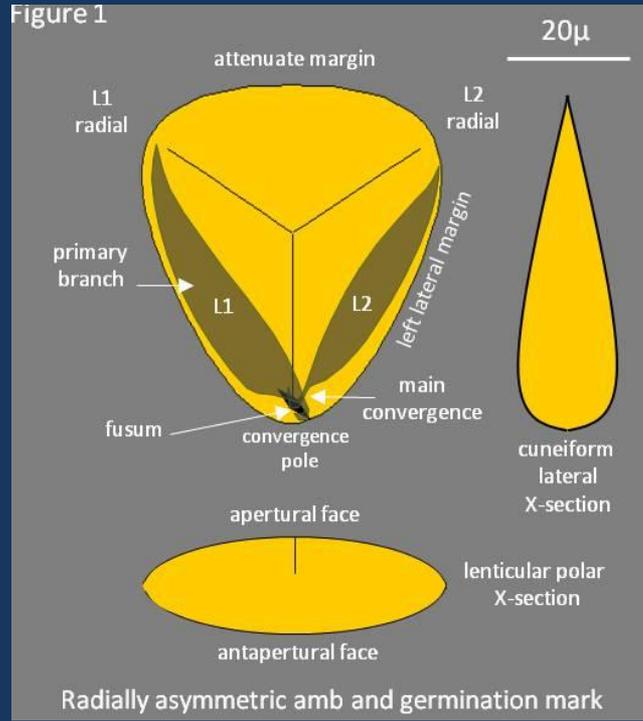
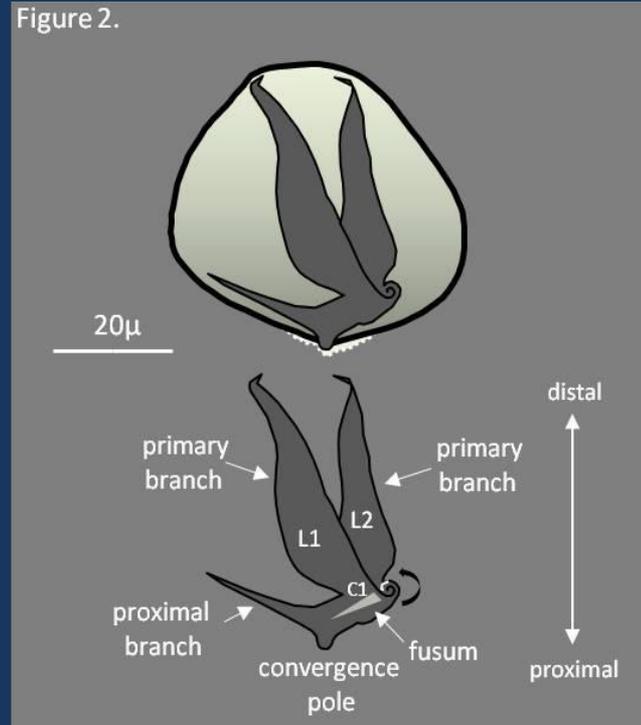


Figure 2.

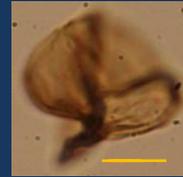


Similar habit in variably mature spores from the same parent plant = "growth sequences"

Biretisporites sp. A - growth sequence



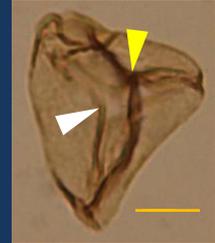
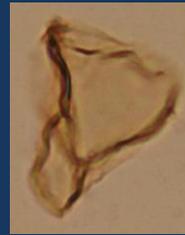
ODS 1



ODS 1-2



ODS 2



ODS 3

bar = 20 μ

more growth sequences 

ODS 1-2



ODS3



Attenuate re-entrant angle

?*Leiotriletes* sp. K

▶ = Transverse element

bar = 20μ



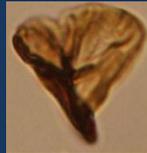
?*Leiotriletes* sp. L



ODS 1

ODS 2-3

ODS 1



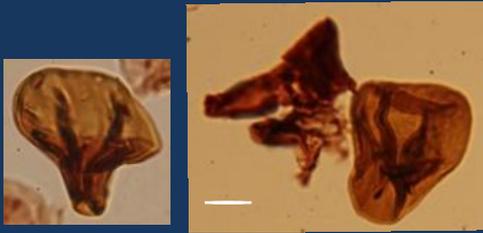
ODS 3



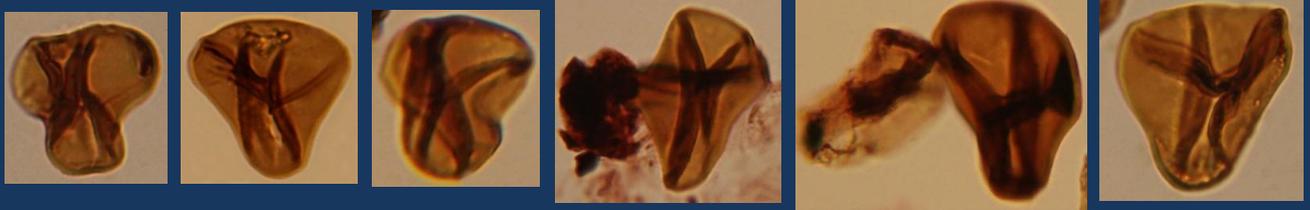
Spore indet B

bar = 20 μ

ODS 1-2



ODS 3



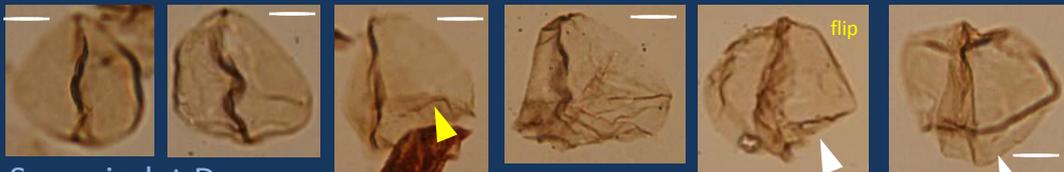
Spore E

bar = 20 μ

Similarities in progressive development in different spores

bar = 20μ

ODS 1

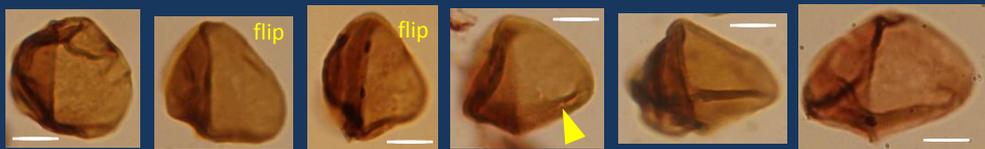


ODS 2

Spore indet D

appearance of perpendicular element

ODS 1

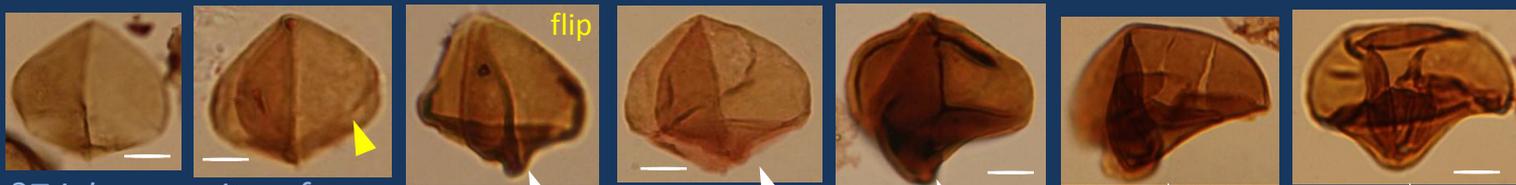


ODS 2

cf. *Triplanosporites manganicus*.

deepening of convergence pole

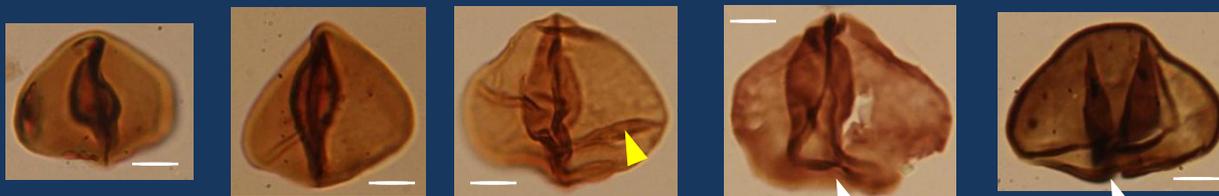
ODS 1



ODS 2-3

?*Triplanosporites cf. couperi*

ODS 1

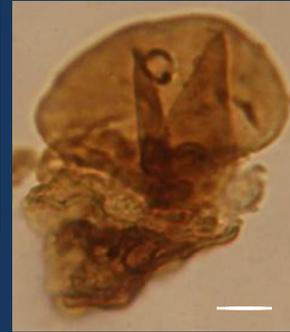
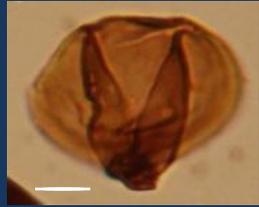


ODS 2-3

cf. *Triplanosporites goczani*

monolateral or bilateral growth

ODS 1



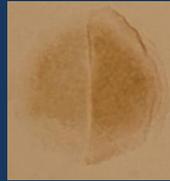
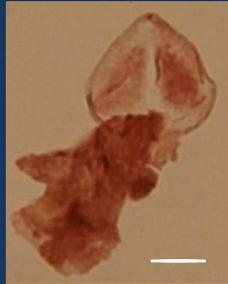
ODS 3



Triplanosporites cf. giganteus

fusum

ODS 1



ODS 2-3

?*Triplanosporites* sp.

bar = 20μ

ODS 1



Spore indet 5

ODS 2-3

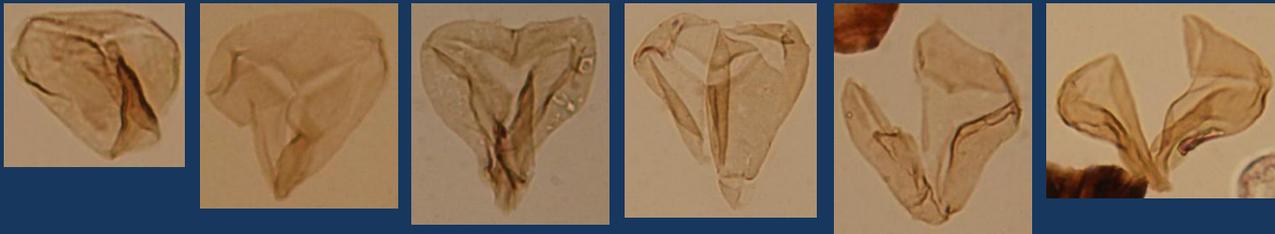


bar = 20 μ — all

ODS 1



ODS3



?*Leiotriletes* sp. Y

ODS 1

ODS3

bar = 20μ — all



Spore indet 6

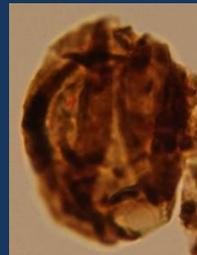
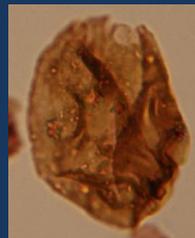
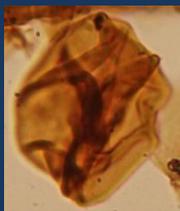
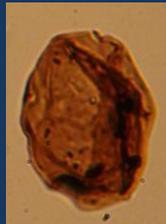
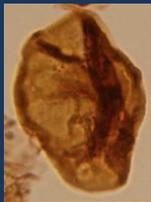
ODS 1

ODS3



Spore indet 8

ODS 1



miospore A

bar = 20μ — all

ODS3

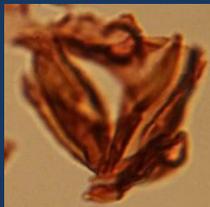
ODS3?



ODS3?



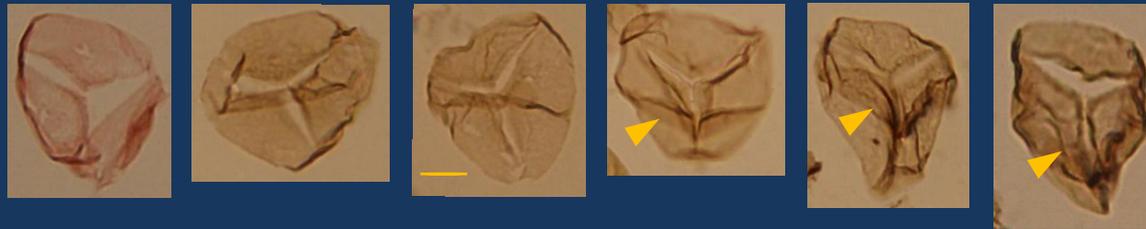
ODS3+?



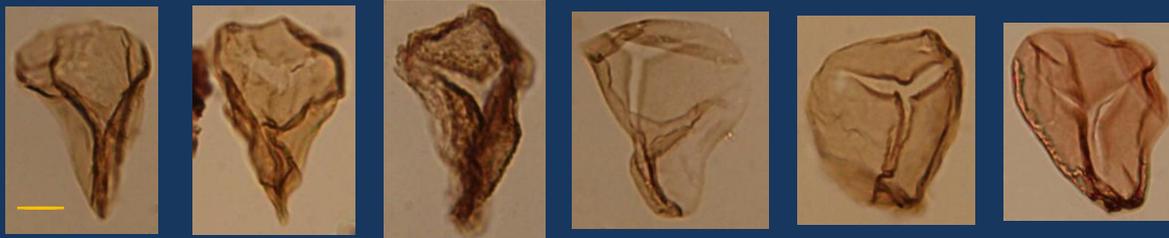
miospore B

No growth sequence yet, though clear similarities in the microfolium

?*Leiotriletes* sp B.



well-developed parallel secondary elements

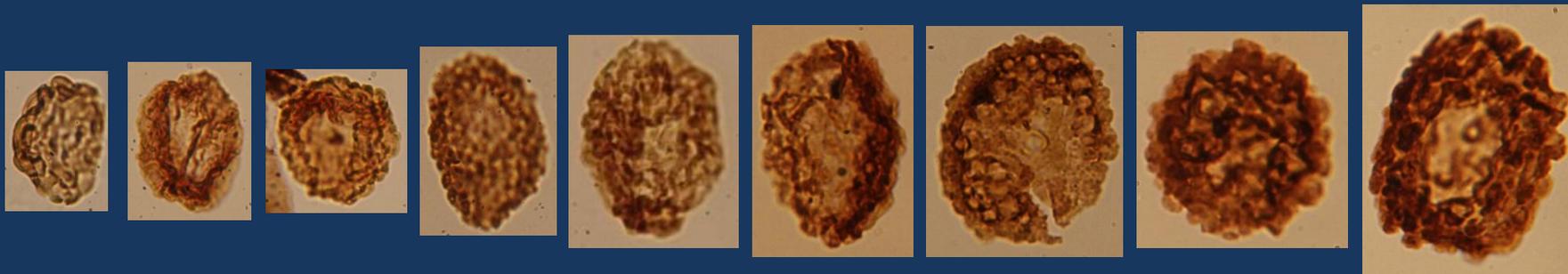


bar = 20 μ

ODS 1

Cerebropollenites macroverrucosus

ODS 3

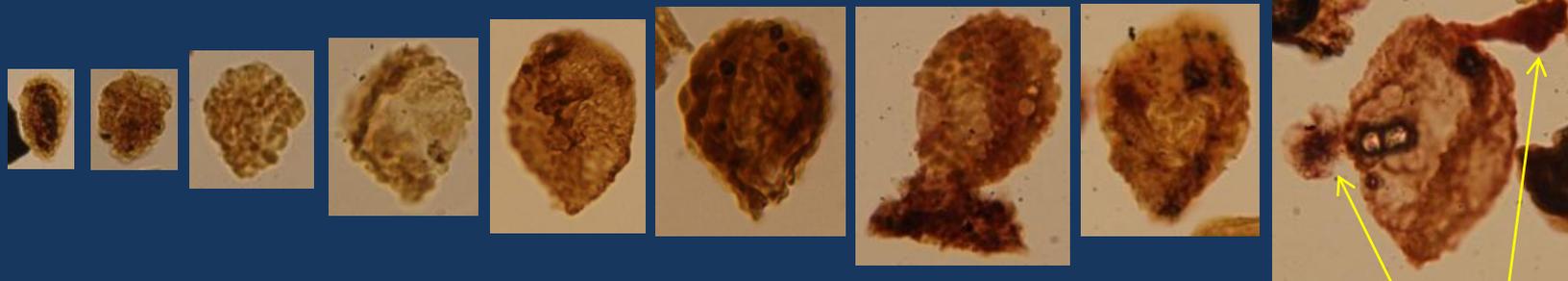


bar = 20μ — all

immature

Gemmae?

mature



"*S. asperum*" sensu BioStrat ; similar to *C. macroverrucosus* and often more common.

propagules

ODS 1



?*Leiotriletes* sp. C.

axial twisting

ODS 3

deepening of convergence pole

ODS 1-2



Leiotriletes sp. E

ODS3

attached via connective element to thalloid structure



bar = 20μ — all

ODS 1-2



ODS3



?*Trilobosporites* sp.

bar = 20μ — all

ODS 1-2

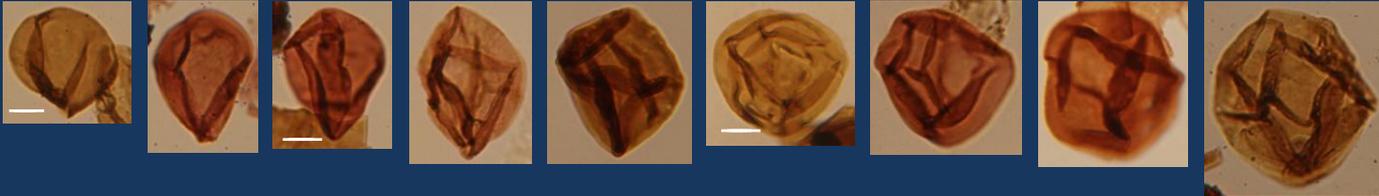


Spore indet. 2

ODS3

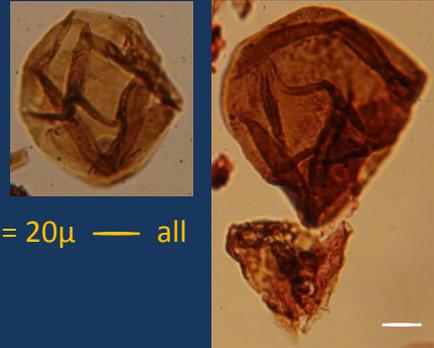


ODS 1



Inaperturopollenites cf. giganteus

ODS 3



bar = 20 μ — all

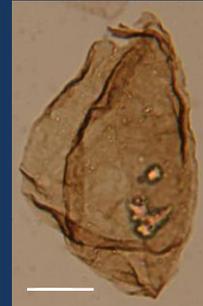
ODS 1



ODS 3



ODS 3+



cf. Laevigatosporites sp.

bar = 20 μ — all

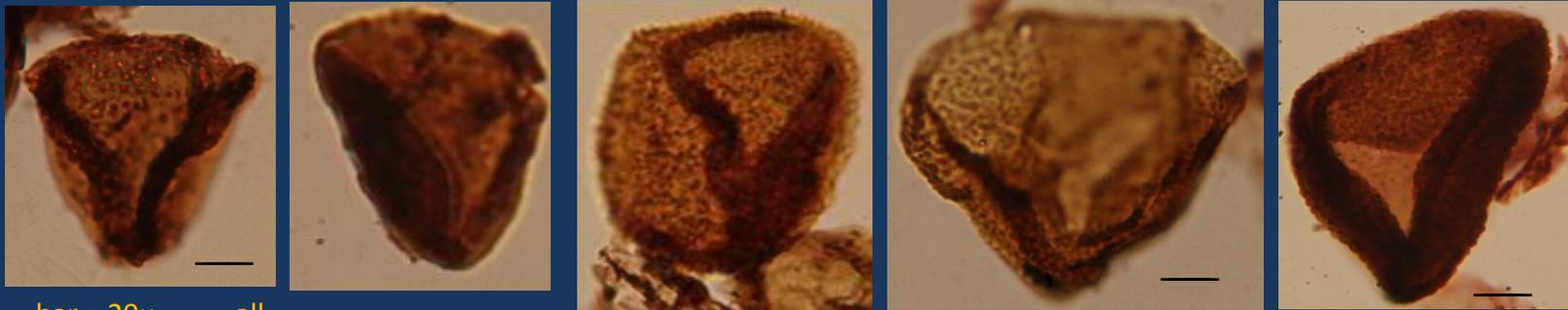
Verrucosisporites cf. cheneyi

ODS 1-2



ODS 3

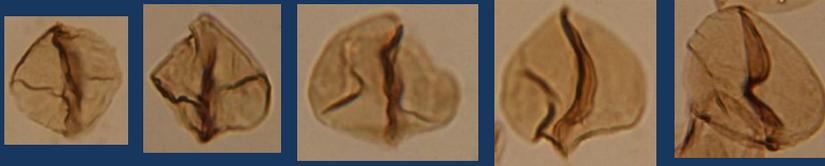
ODS 3+



bar = 20 μ — all

Other life cycles; Attached reproductive cells - ARCs

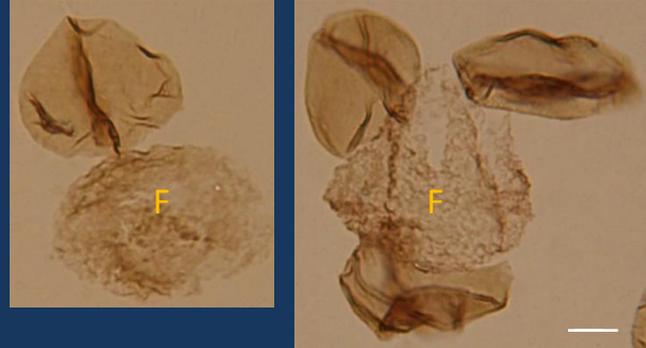
ODS 1 (equivalent)



Spore indet. A

bar = 20 μ — all

ODS 3

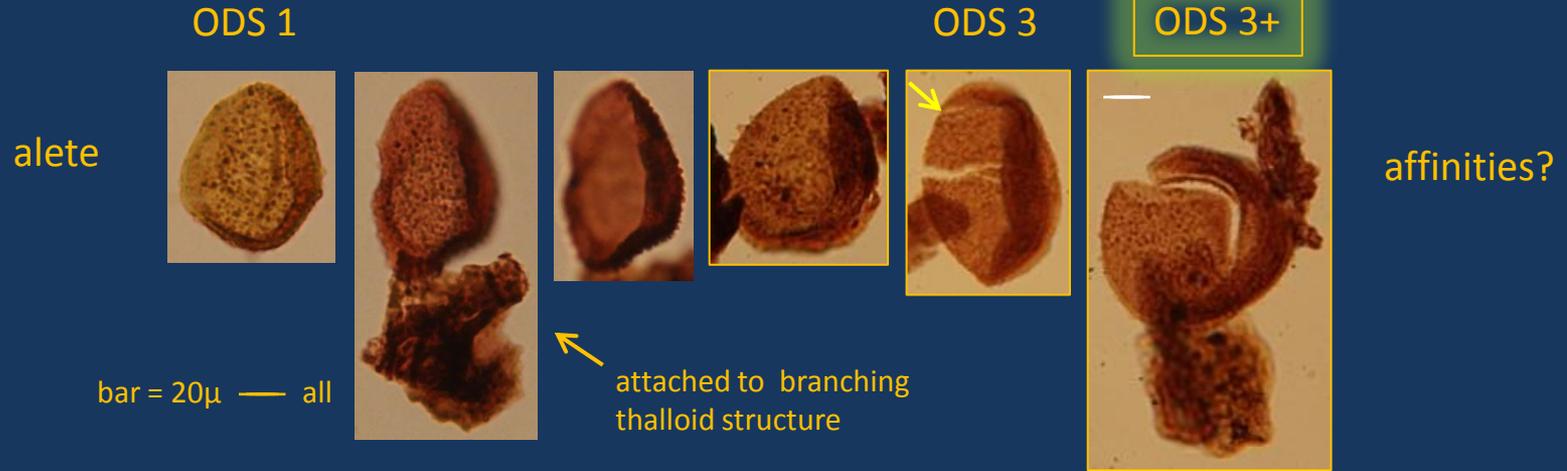


❖ attached to “fruiting cell”

❖ clues to life cycle?

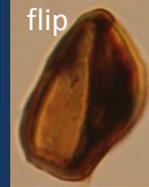
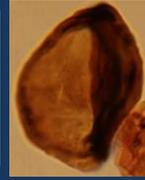
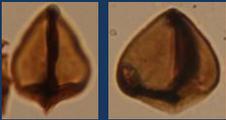
Other life cycles; Attached reproductive cells - ARCs

?*Conaletes* sp.



Attached reproductive cells - ARCs

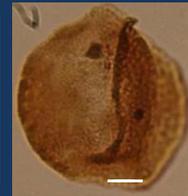
ODS 1



ODS 3

cf. *Matonisporites* sp.
or spp. ?

ODS 1



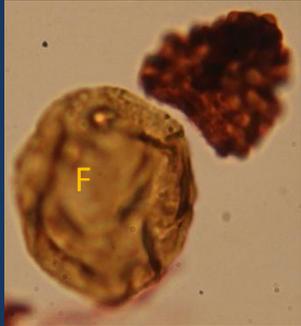
ODS 3

bar = 20μ — all



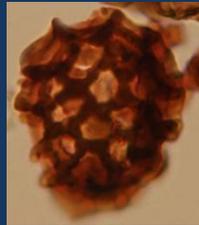
Attached reproductive cells - ARCs

ODS 1



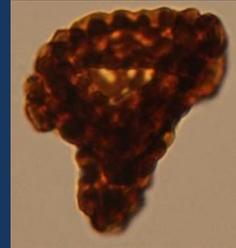
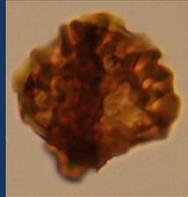
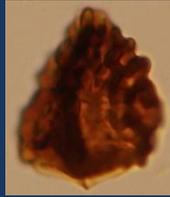
bar = 20μ — all

ODS 1



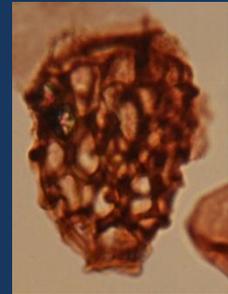
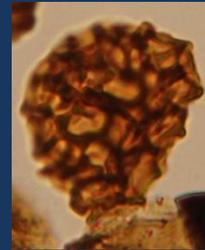
Ischyosporites "latimurus" BioStrat

ODS3

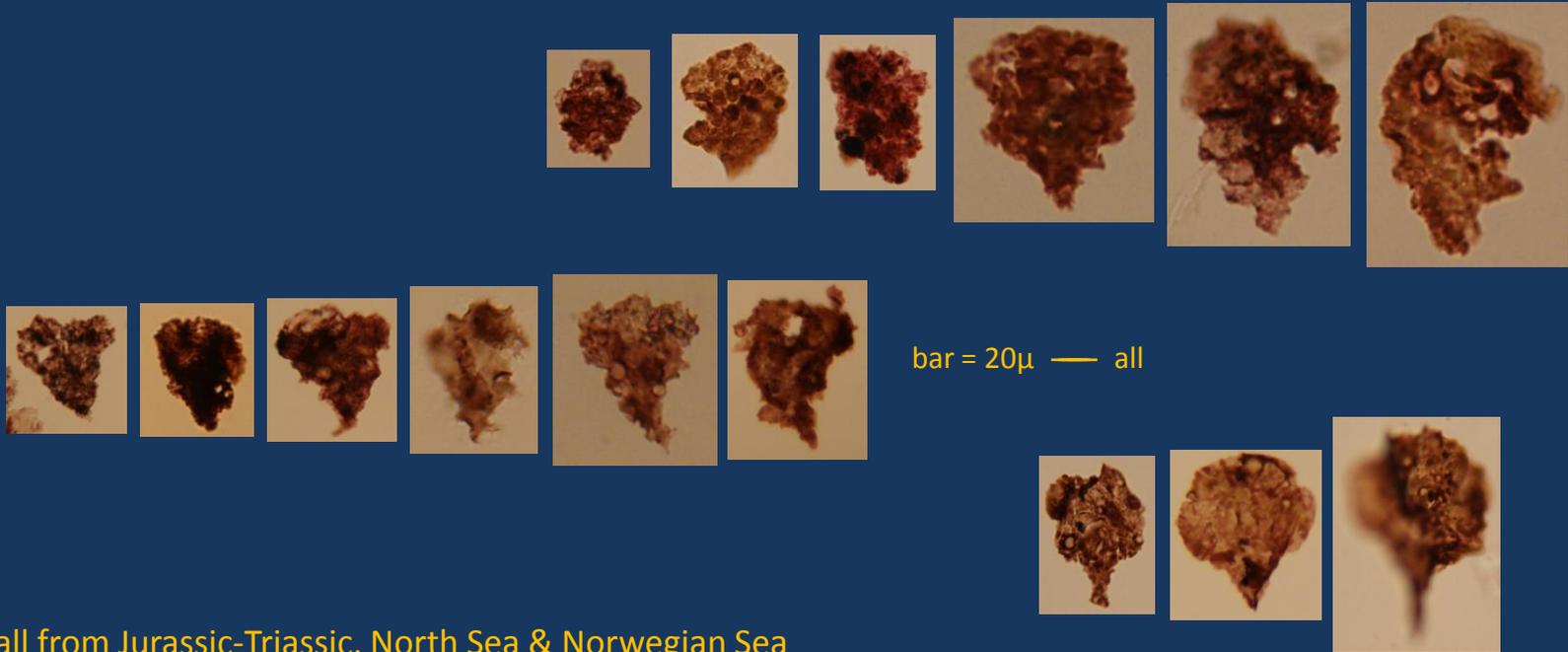


thalloid cell? or protonemal tissue?

ODS3



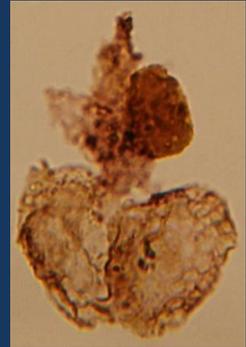
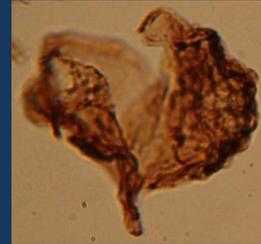
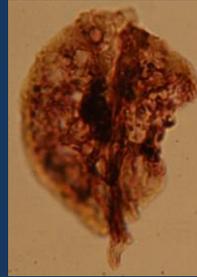
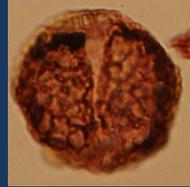
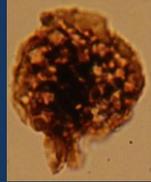
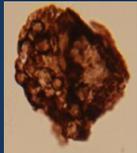
Other life cycles; gemmae of hepatic plants



all from Jurassic-Triassic, North Sea & Norwegian Sea

Other life cycles; Attached reproductive cells - ARCs

Bisaccate-like ARC develops longitudinal split

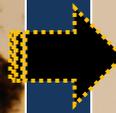
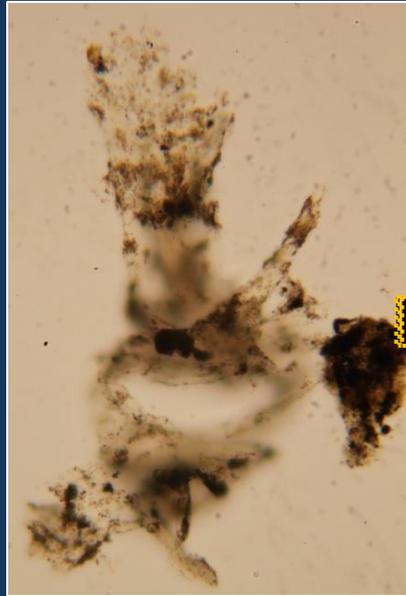
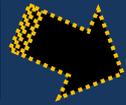


immature

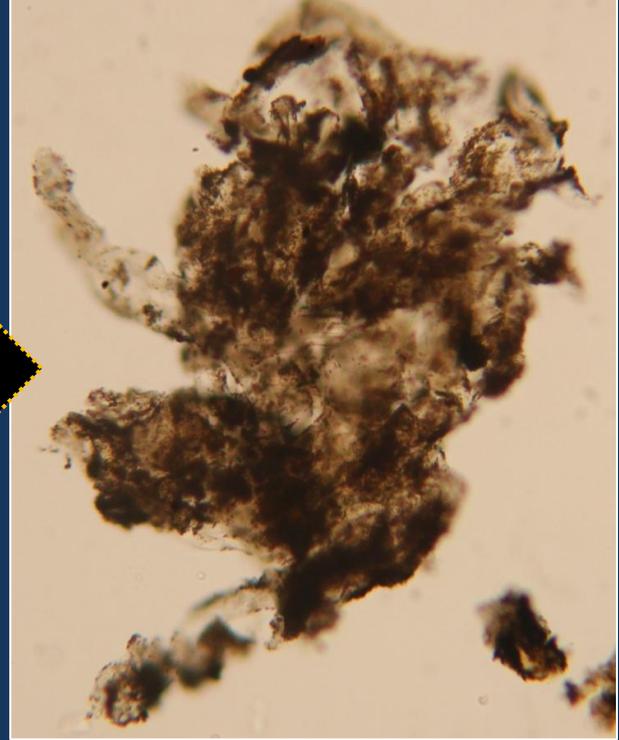
mature

bar = 20 μ — all

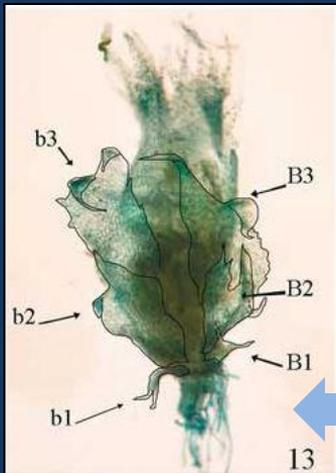
Other life cycles; "fruiting growth"



Jurassic, North Sea



500 microns



13

Gynoecium of *Octoscyphus crassicaulis* (extant liverwort), with bracts and bracteoles highlighted. Figure 13 in: Engel *et al.* 2012.

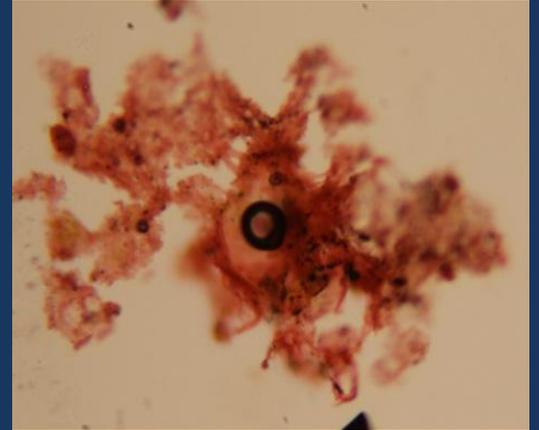
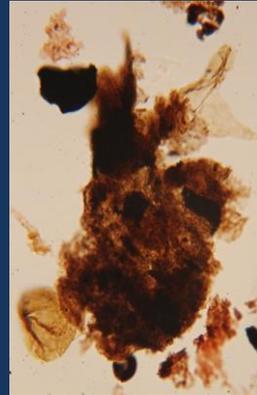
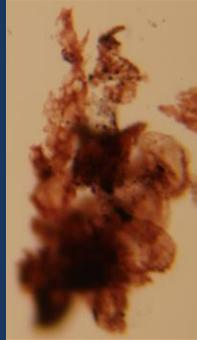
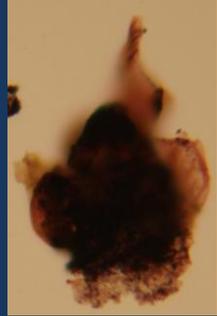
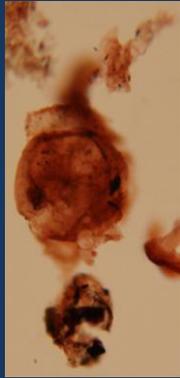
500 microns

Other life cycles; “fruiting growth”

immature



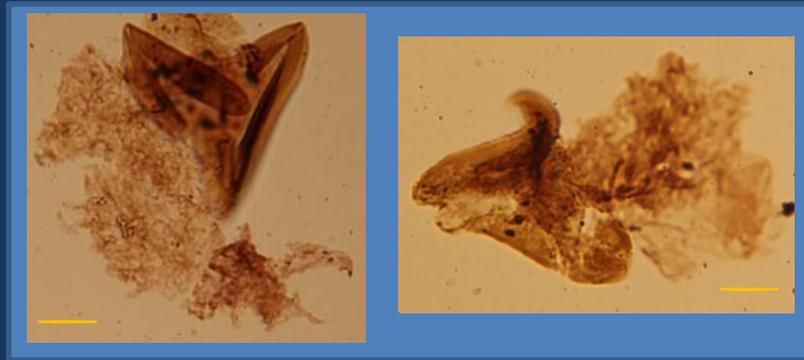
mature



250μ

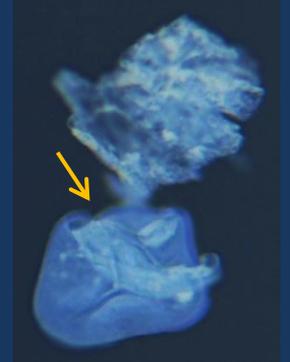
Possible gynoecium or perianth of a liverwort. Jurassic NNS

In dispersed assemblages further morphological variability is caused by rupturing of the cell wall during germination/dehiscence.



“Normal” spore germination

Other types of wall rupturing observed in many spore-like cells, -
inconsistent with “normal” germination. - *dehiscent cells*



Teichertodium triassicum
Stover & Sarjeant 1972

bar = 20 μ

cell contents do not
emerge through
germination aperture

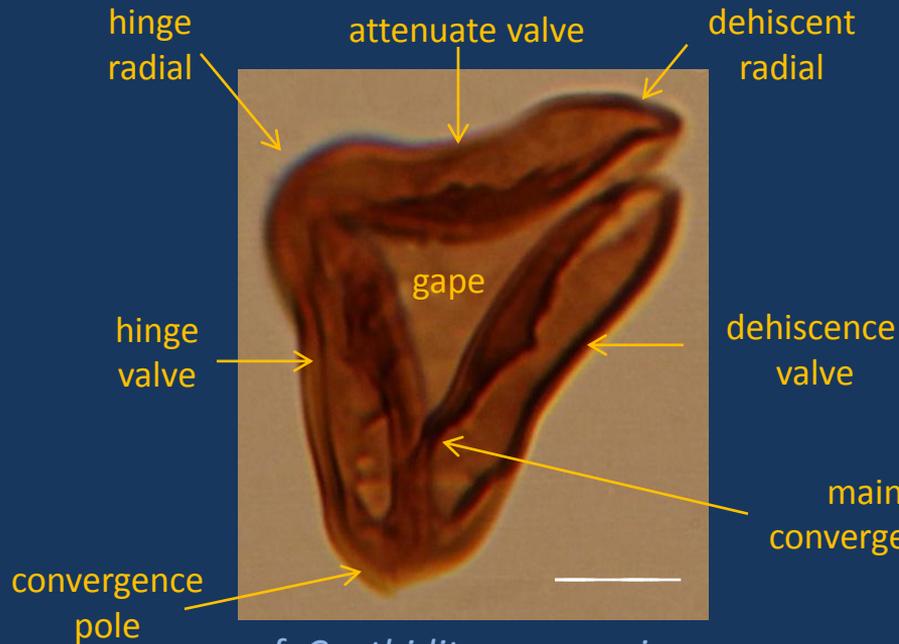
Wide variety of dehiscent spore-like cells reflect more diverse life cycles

Dehiscent spores - unknown affinities

Rupturing continues onto antapertural surface

monolateral dehiscence

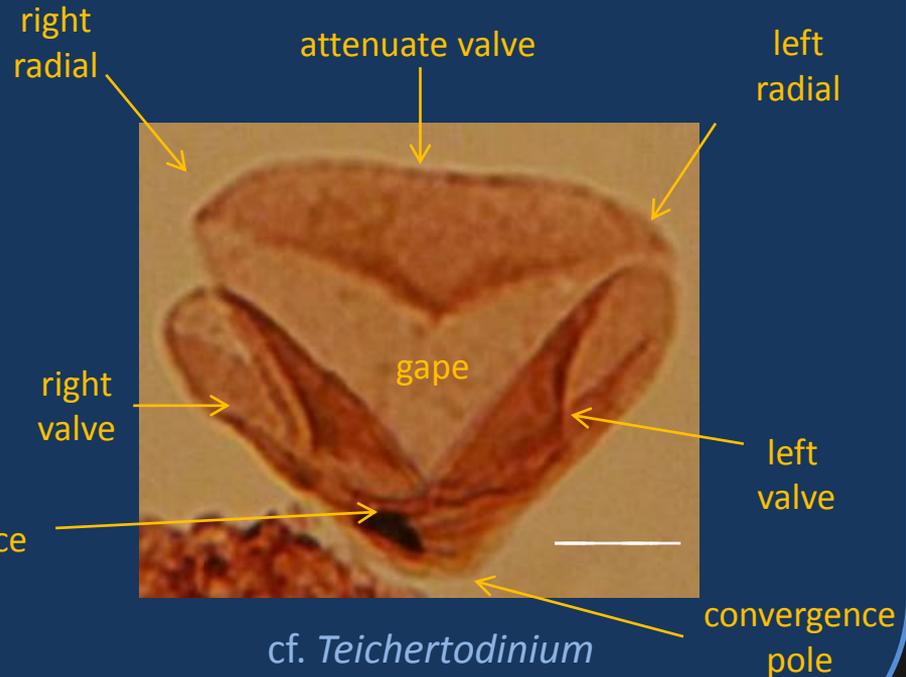
cell remains entire



cf. *Cyathidites mesozoicus*
sensu Na *et al.* 2014

bilateral dehiscence

attenuate valve commonly lost



cf. *Teichertodinium*
Pocock & Sarjeant 1972

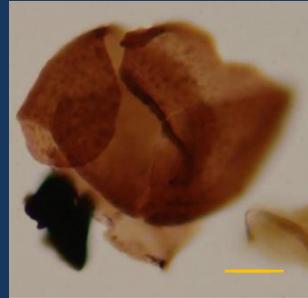
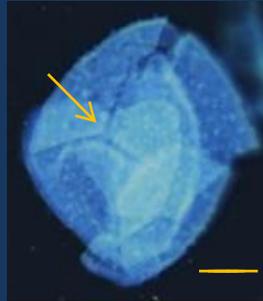
bar = 20 μ

Dehiscent spores

Teichertodinium triassicum Stover & Sarjeant 1972



bar = 20 μ

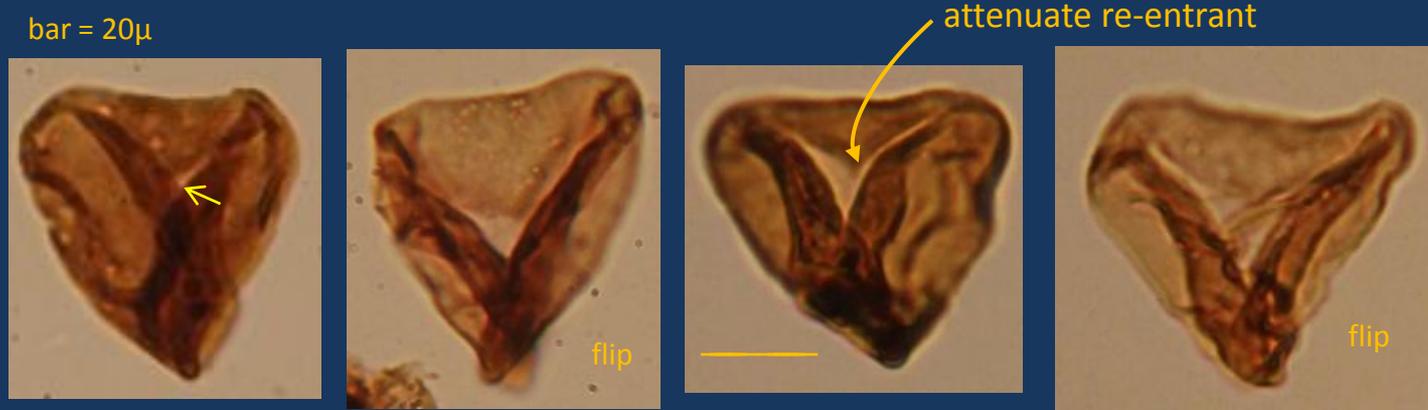


Published as an acritarch

Spore-like, including trilete mark

ARC – attached reproductive cell

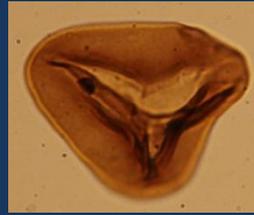
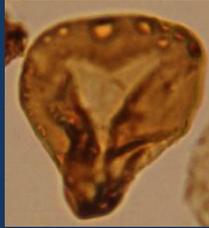
“Bilete” gaping aperture; - ?affinities



Splitting initiates from point inside divergence of lateral branches (*yellow arrow*), gradually extending in two directions towards attenuate radials.

Gaping apertures

ODS 1-2



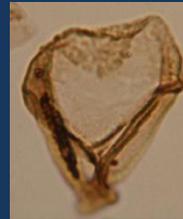
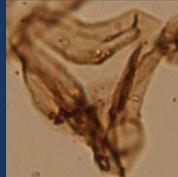
ODS3

bar = 20 μ — all

?*Cyathidites* sp. A

★ Rupturing restricted to apertural face. ★

ODS 1-2



ODS3

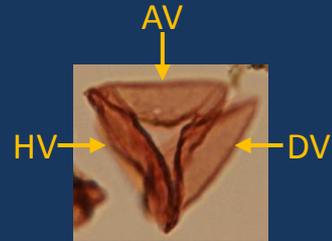
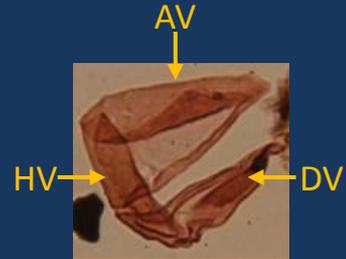
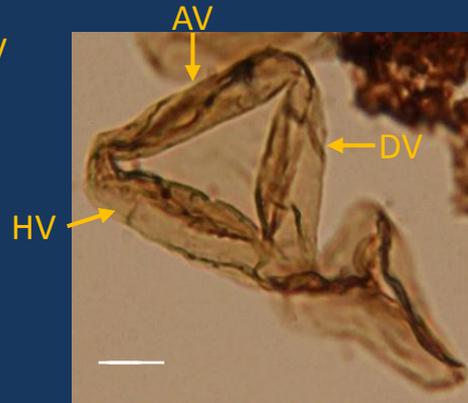
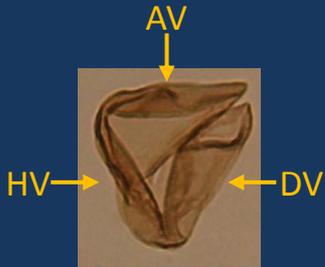
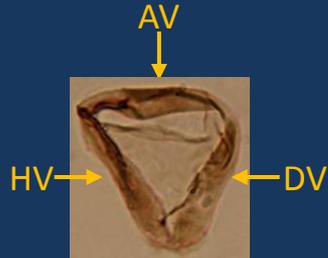
?*Leiotriletes* sp. F

Aperture becomes larger, with relatively little associated increase in cell size

Not mature until gape fully formed

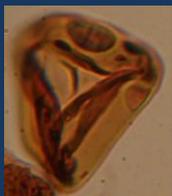
Dehiscent spores

Monolateral dehiscence

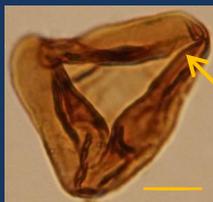


Monolateral dehiscence

ODS 2-3



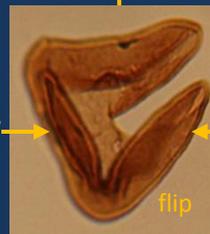
ODS 3



ODS 3+



AV



HV

DV

flip

flip

Cyathidites mesozoicus sensu Na et al. 2014

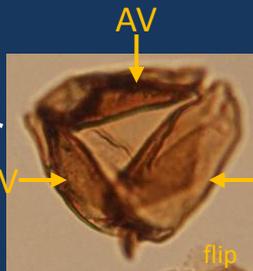
bar = 20μ

★ rupturing extends around dehiscent radial onto the antapertural face

ODS 3



ODS 3+



HV

DV

AV

flip

★ cell remains entire

Cyathidites cf. mesozoicus sensu Na et al. 2014

ODS 3



Cyathidites mesozoicus sensu Na et al. 2014 (rotated)

Monolateral dehiscence

ODS 1-2



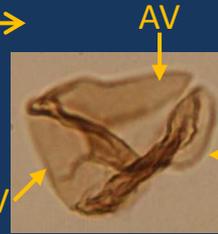
ODS 2



ODS 3



ODS 3+ →

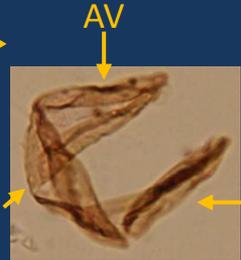


?*Leiotriletes* sp. G

ODS 3



ODS 3+ →



distinctive diagonal split
with folded margins on
antapertural surface

?*Leiotriletes* sp. H

bar = 20μ — all

Monolateral dehiscence

immature



mature



Indeterminate
spore-like cell

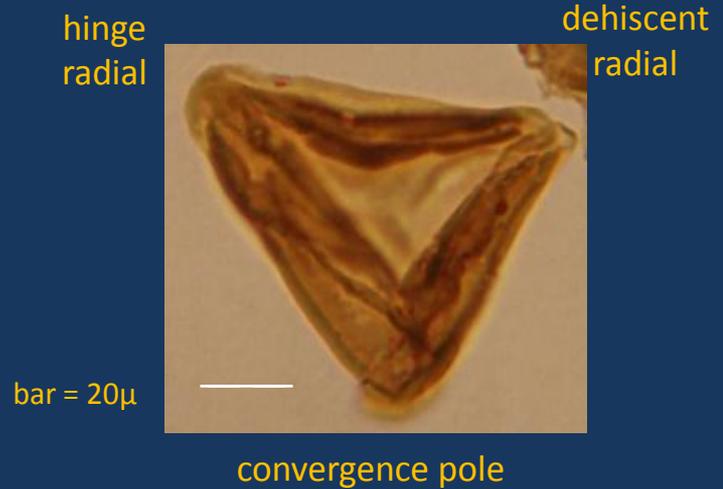
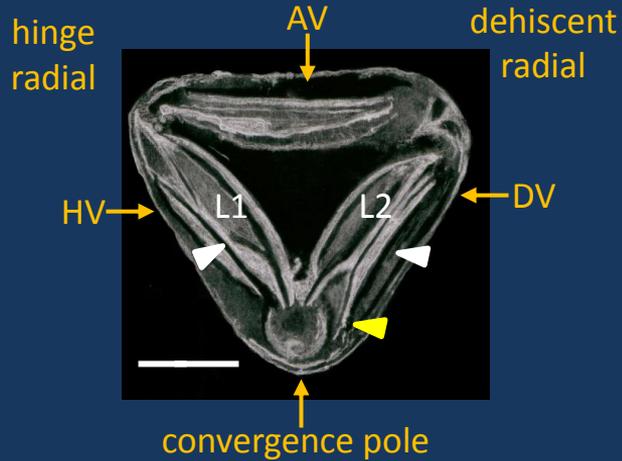


all mature?

bar = 20 μ — all

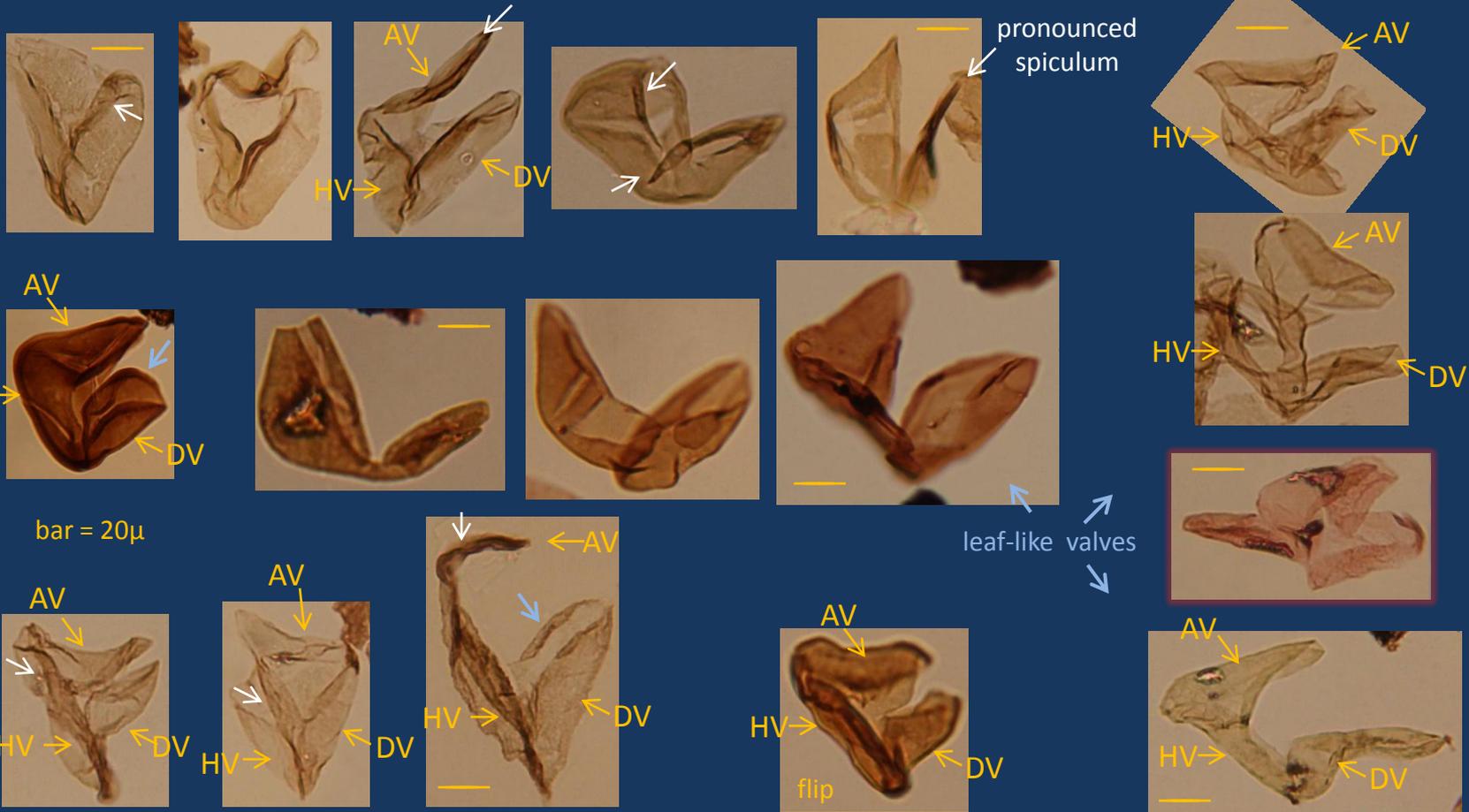
Monolateral dehiscence

Even before dehiscence occurs



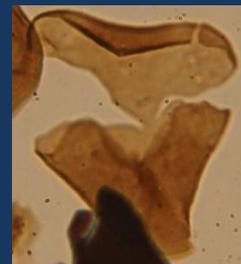
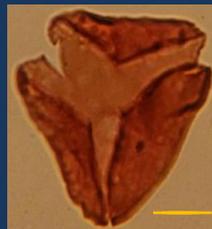
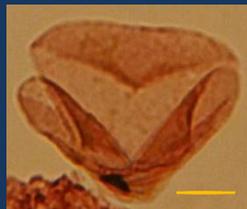
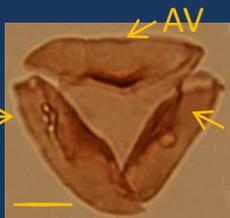
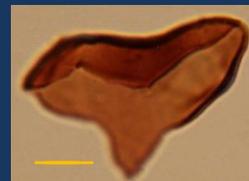
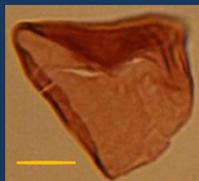
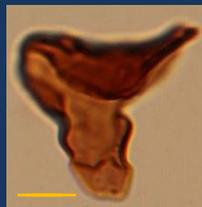
Cyathidites minor sensu Tahoun and Mohamed, (2014, Figure 3.11 (300°)).
Scale bar 10 μ , Jurassic.

Monolateral dehiscence in unknown spore-like cells



Bilateral dehiscence

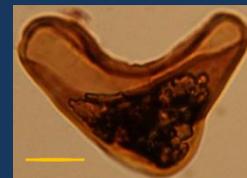
cf. *Teichertodium* Pocock & Sarjeant 1972



?*Teichertodium* sp. A

?*Teich.* sp. D

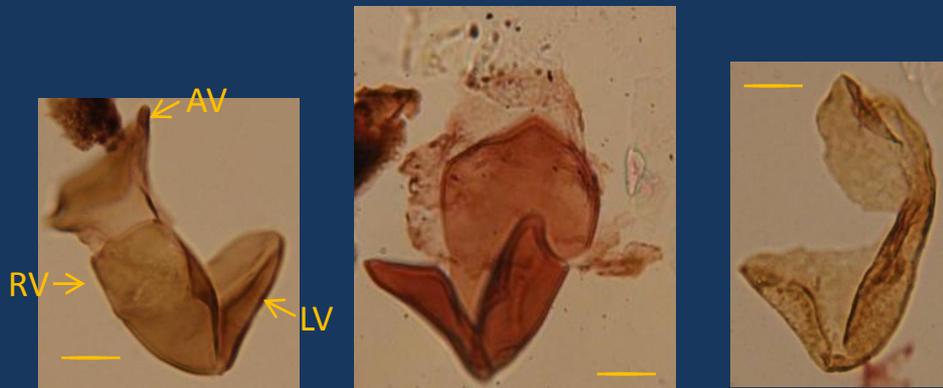
?*Teich.* sp. E



bar = 20μ

Rupturing extends around both attenuate radials onto antapertural face.
Attenuate valve may remain attached, though commonly lost

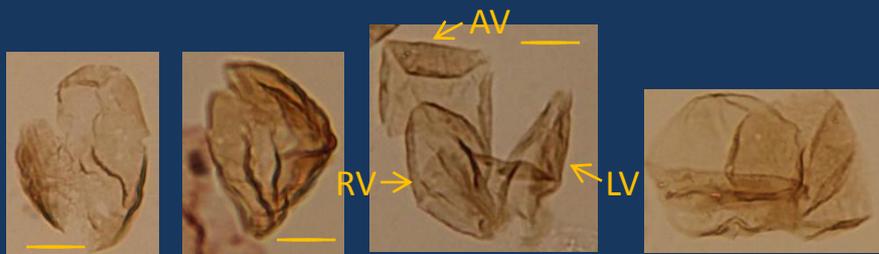
Bilateral dehiscence



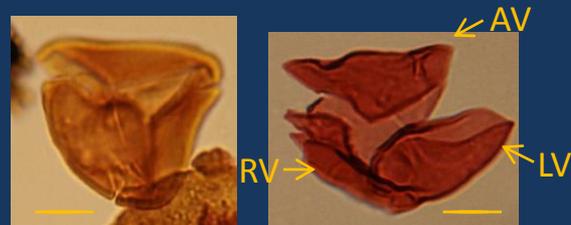
attenuate valve fully
operated, still attached

bar = 20 μ

?*Teichertodinium* sp. A



?*Teichertodinium* sp. B



?*Teichertodinium* spp.

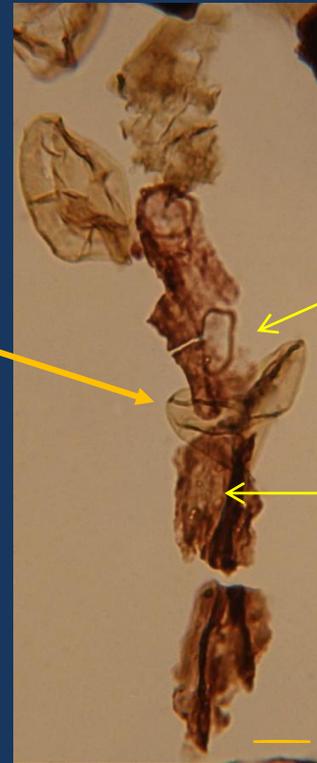


!!!?

?*Biretisporites* sp. A



?*Teichertodium* sp. A

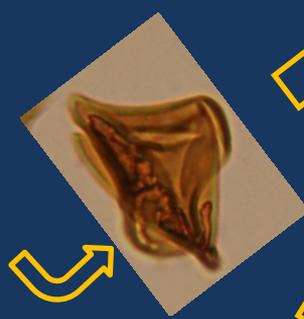


bar = 20 μ

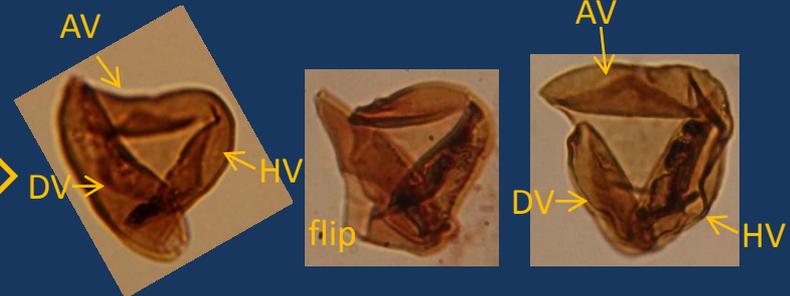
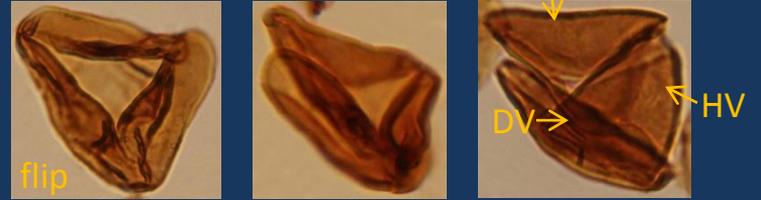
The microfolium is related to the internal structure, shape & growth of the cell



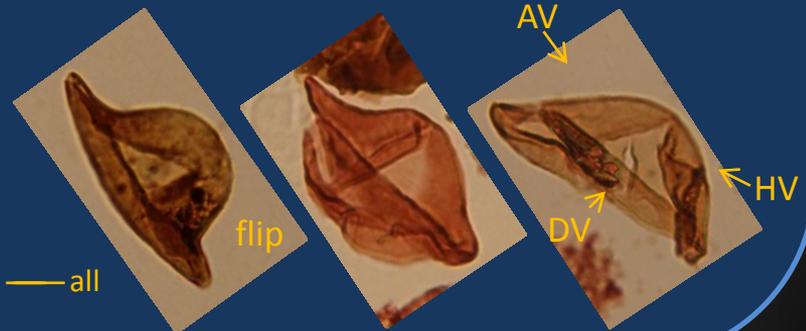
?Spore indet D



Equivalent "branches" & valves

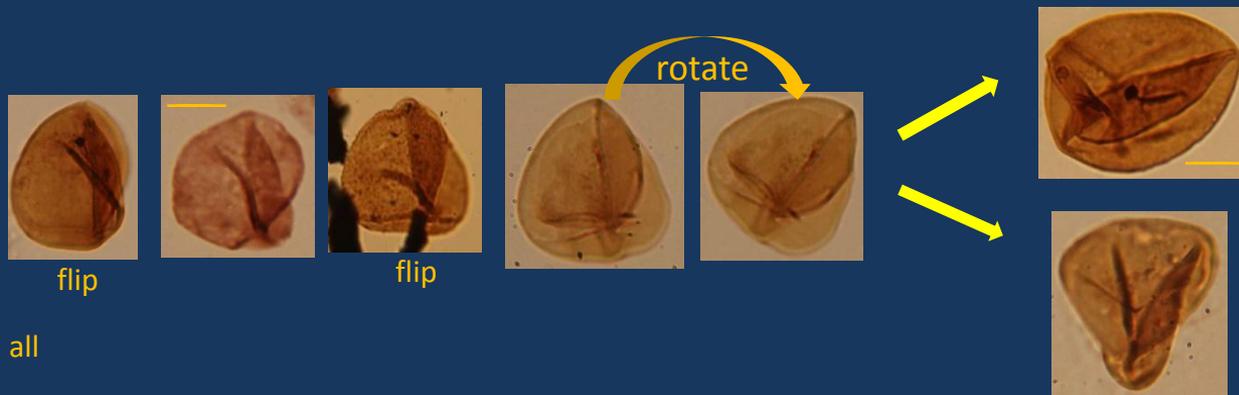


And to rupturing of the cell wall during germination/dehiscence



bar = 20μ — all

Branch equivalence $A_x \text{ \& } P_x = L1 \text{ \& } L2$



bar = 20 μ — all



Organism indet A



Why have a trilete mark?

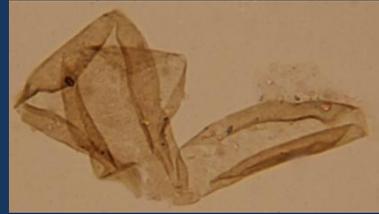
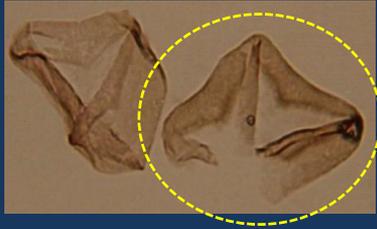
immature



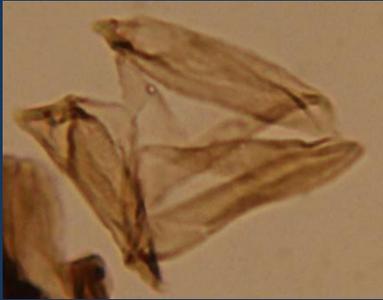
flip



Organism indent B
a leafy liverwort?



bar = 20μ — all



← mature? →

Conclusions

- Current models for the description of fossil miospores do not sufficiently consider or accurately reflect the variety of life cycles in ancient plant communities
- Nor the significant morphological variation in spores produced by a single plant species
- The microfolium is fundamental to the internal structure of many fossil plant/algal reproductive cells.
- Offers strong potential as a high-ranking morphological feature in taxonomy and classification.
- The microfolium has a similar “habit” in variably mature microspores produced by a single plant.
- Input of botanical expertise required:- living representatives, life cycles