

**New observations on Mesozoic miospores and
acritarchs, and the implications for existing
taxonomy, classification and phylogeny.**

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Thanks to



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Jurassic non-marine assemblages

Traditional view

Low diversity microfloras with **few** reliable stratigraphic markers.

Relatively simple, well established ecological model, e.g. Abbink et al 2004.

However, not all in the garden is rosy.....

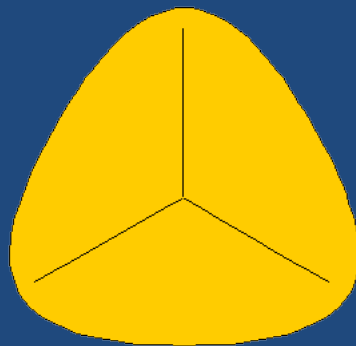
Miospore systematics and taxonomy are over-simplified.

Our current models do not reflect the numerous and varied life-cycles of lower plants.

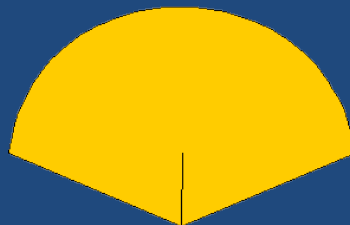
Neither do they consider, or reflect morphological changes due to growth or sexual maturity.

Applications.....

Trilete spores



Proximal Polar
view

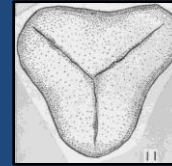


Distal surface

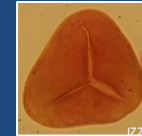
Proximal surface

lateral view

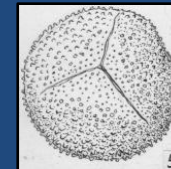
Cyathidites/Deltoidospora



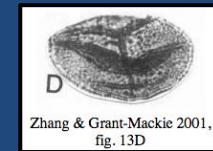
Cyathidites australis
Couper Drawing of
holotype



Osmundacidites/Baculatisporites



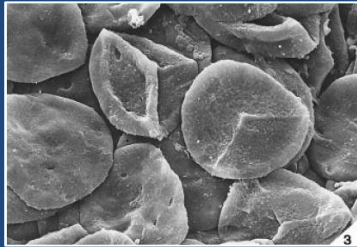
Osmundacidites welmanii
Couper Drawing of holotype



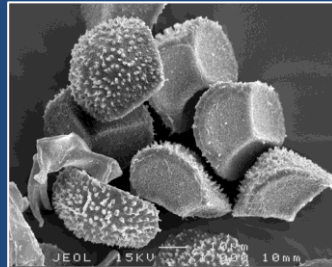
Zhang & Grant-Mackie 2001,
fig. 13D

The general assumption has been trilete mark on proximal surface, reflecting contact with other members the tetrad. (Playford & Dettman 1996).

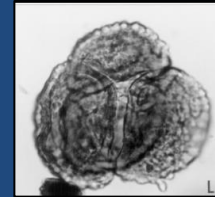
Trilete mark does not always reflect tetrad



Spores of *Scylaspora*. Early Devonian. From Wellman 1999, pl.1, fig.3.



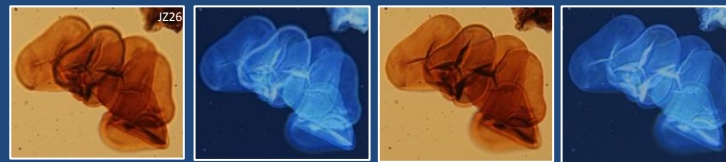
Phaeoceros carolinianus, an extant hornwort. Fig. 12 in Glime 2013



Tetrad of *Uvaesporites verrucosus*. From de Jersey & Raine 1990, pl.3, fig. L. in Raine *et al.* 2011. Triassic



Granulatisporites infirmus Plate 2, fig. 1 in Cornet & Traverse 1975. Hettangian

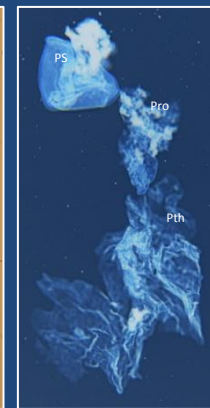
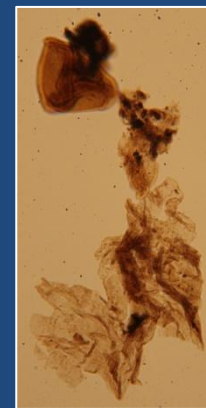
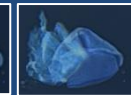
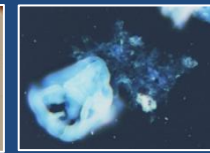
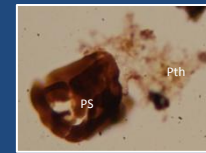
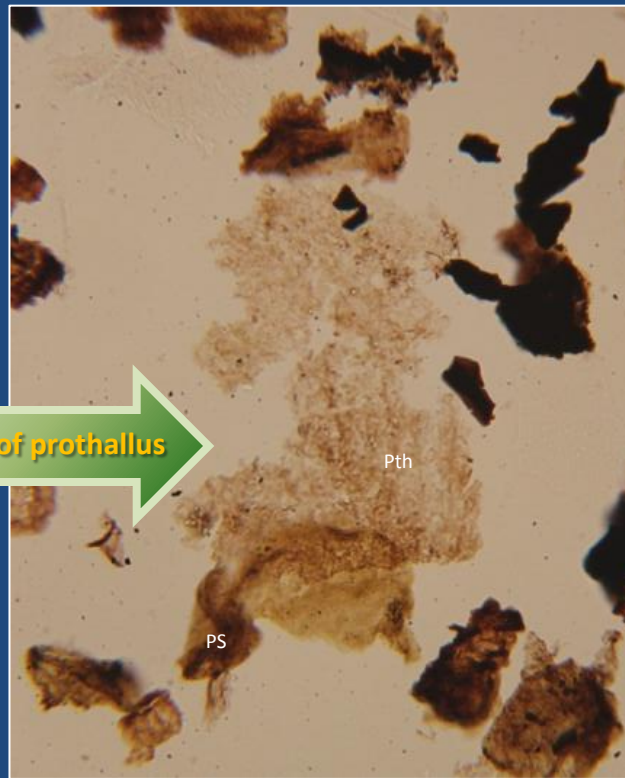
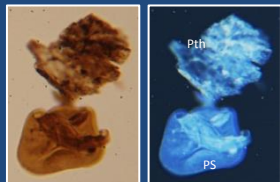
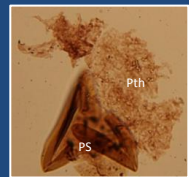
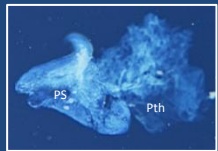
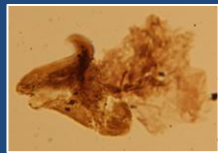


?*Cyathidites* sp. Hugin Formation Late Callovian NNS



All are dispersed reproductive cells and produced within a sporangium.

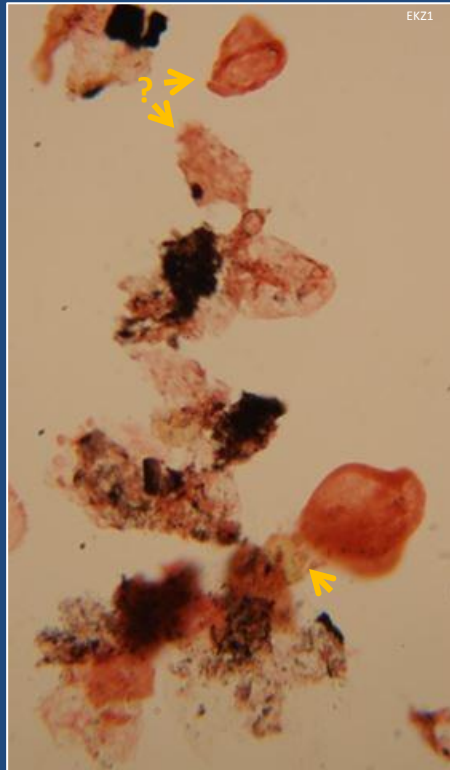
Evidence of germination in fossil spores



Early and Middle Jurassic , NNS

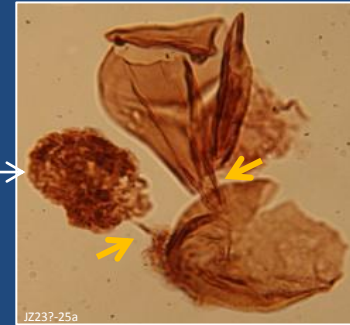
PS Primary spore
Pth Prothallus (gametophyte)

Attached sporomorphs



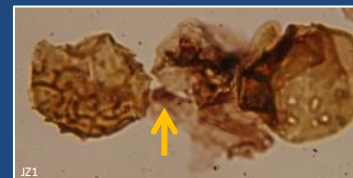
Upper Draupne Formation (Berriasian), SVG

immature?
sterile? →



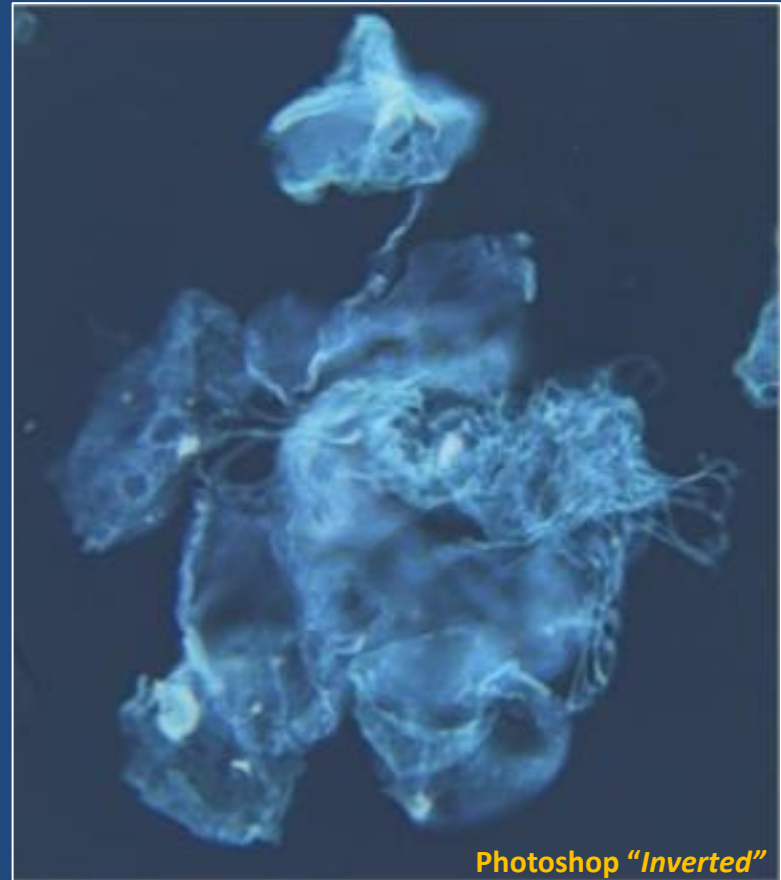
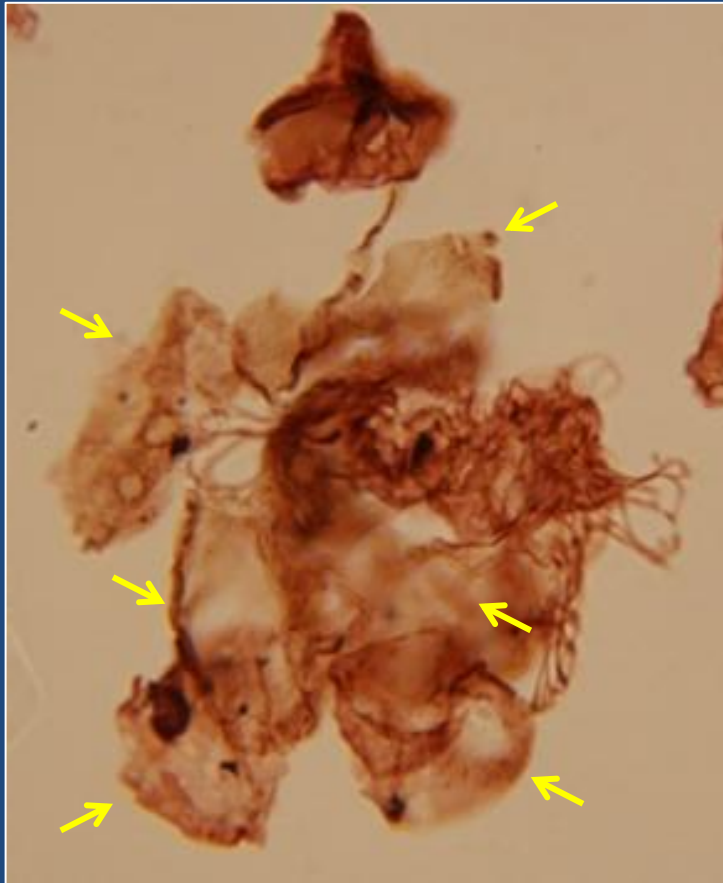
Cyathidites-like cell. Hugin Formation (Callovian), South Viking Graben

250μ



Retitriteles-like cell. Åre Formation (Early Hettangian), Norwegian Sea.

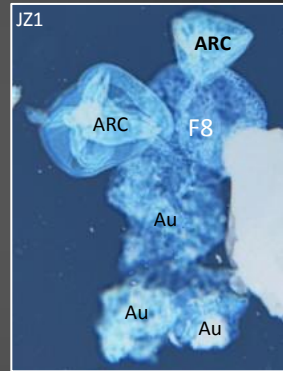
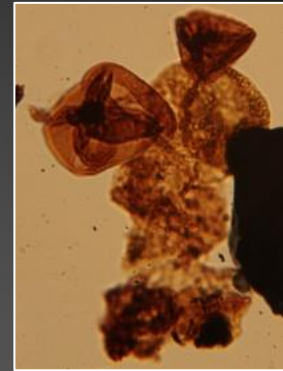
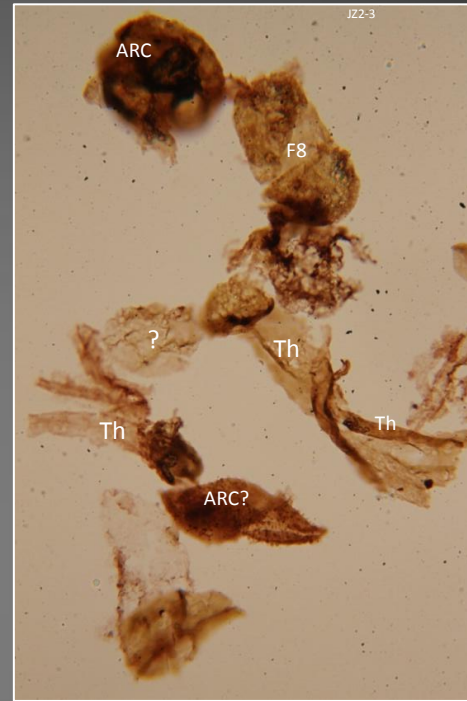
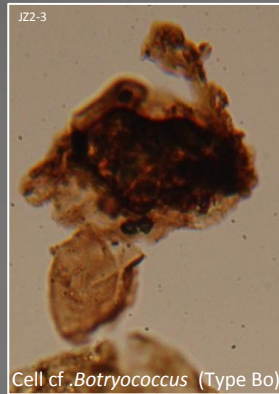
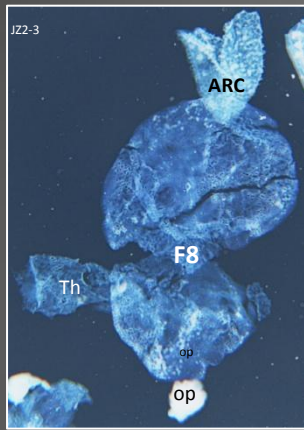
Cyathidites-like cell attached to a twin skolochorate cell.



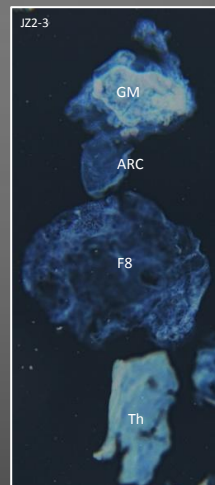
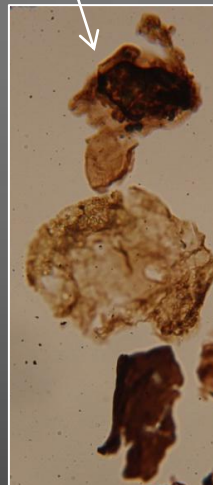
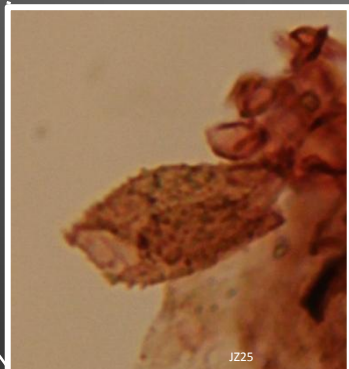
Heather Formation (Callovian), SVG

Attached reproductive cells, NOT dispersed spores.

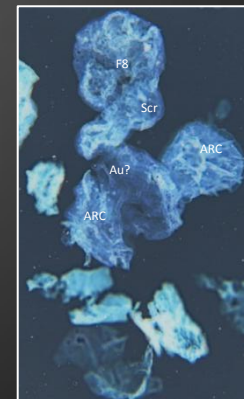
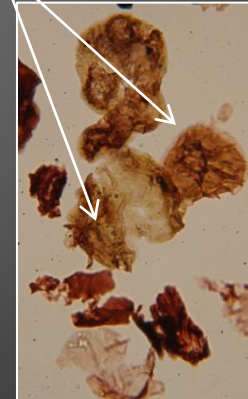
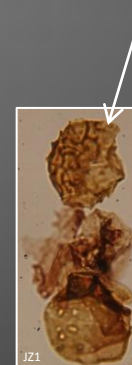
ARC Attached reproductive cell
F8 F8 cell
Th Thalloid cell
GM Gamete mass?
Op opaque cell



500μ



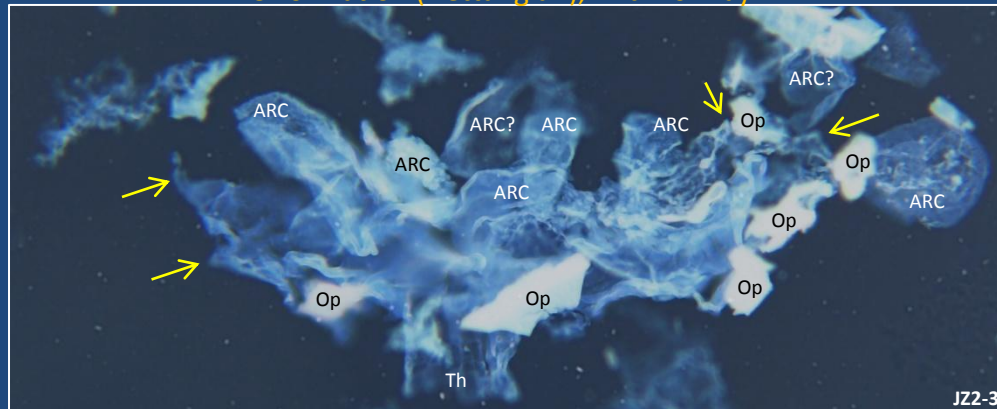
cf. *Retiriletes* (Type Ra)



Fruiting structure with numerous attached reproductive cells in various stages of maturity.



Åre Formation (Hettangian), Mid Norway



ARC Attached reproductive cells
Op Opaque cells

500μ

For the present, use the loose term; “attached reproductive cells” (ARC)

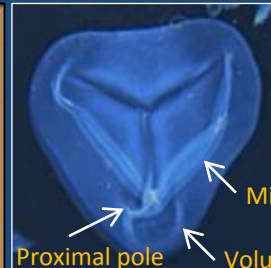
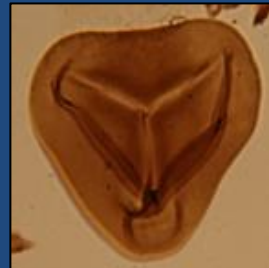
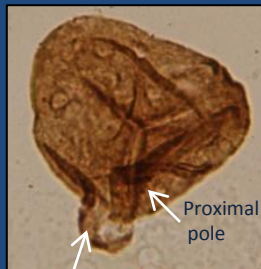
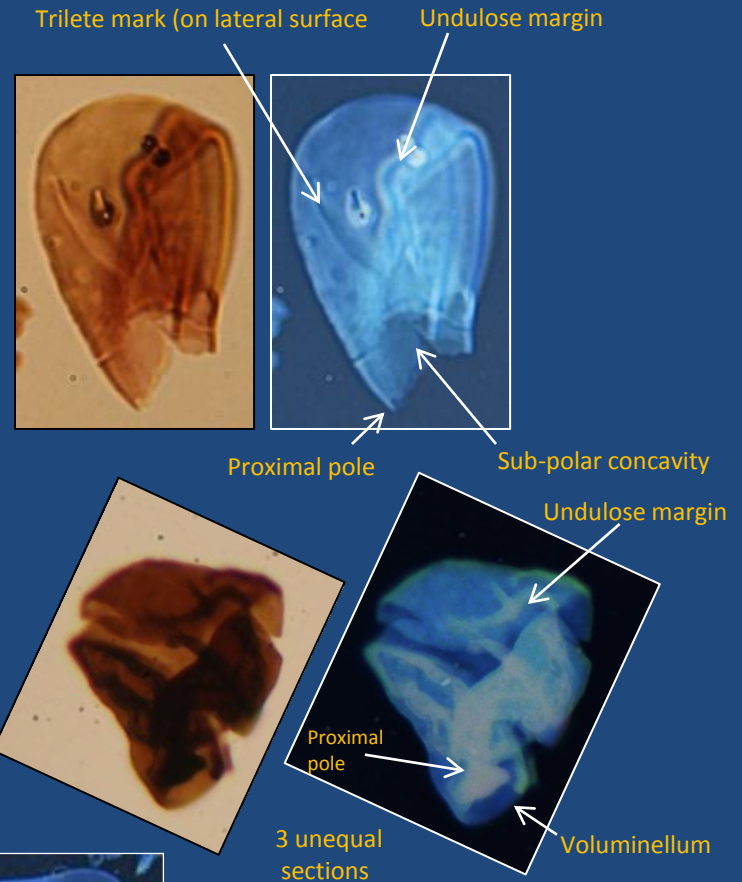
Morphology of attached reproductive cells.

PRIMARY FEATURES:

- Attachment structure.
- Attachment to host cell at proximal pole.
- Exhibits growth.
- Trilete mark (if present) on distal or lateral surface.

SECONDARY (variable) FEATURES:

- Voluminellum (scroll) developed at proximal pole.
- Splits into 3 unequal sections.
- One section commonly with an undulose margin.
- Other modes of rupturing.
- Microfolium.
- Sub-polar concavity.
- Generally does not exhibit radial symmetry.



Microfolium

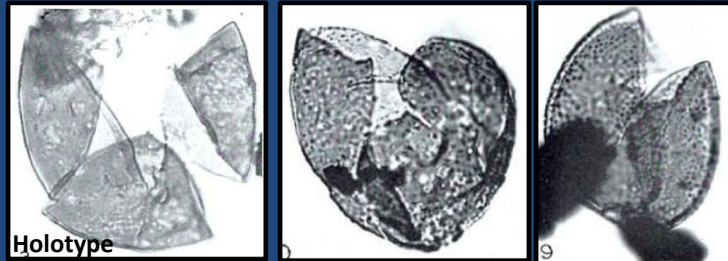
Voluminellum

Teichertodinium Pocock & Sarjeant 1972

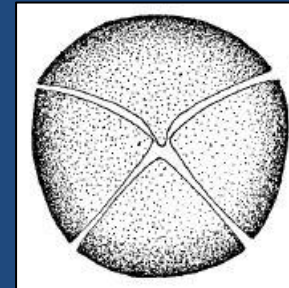
Original diagnosis is rather vague and not substantiated by illustrated specimens

Diagnosis (from Pocock & Sarjeant 1972):
“Vesicle spheroidal to broadly ovoidal; wall two-layered. The vesicle divides into four sections. The main body divides into three sections of closely similar size and shape (though the antapical section may differ slightly from the two lateral sections). The apical cap is of comparable size, but differs in its possession of two “tongues” fitting into the space at the point of junction of the three main-body sections (see text-fig. 3). The surface may be psilate or faintly punctate or may be covered with closely spaced, low granules or more widely spaced, enlarged granules or short baculae (see plate 3). In psilate forms, the wall is relatively thin: the forms with more marked ornamentation are also thicker-walled”.

Teichertodinium triassicum Triassic Type material

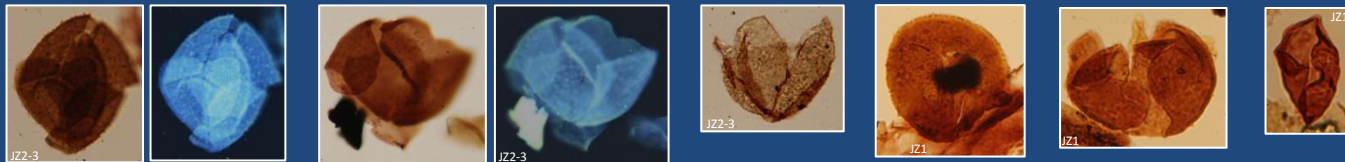


from Pocock & Sarjeant 1972



Text-fig. 3 in Pocock & Sarjeant 1972

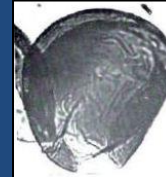
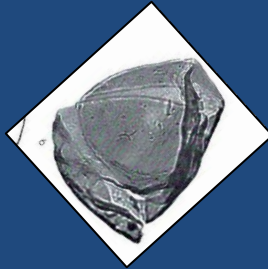
Teichertodinium triassicum from Late Triassic and Jurassic, NNS



Rugidinium Pocock & Sarjeant 1972

Original diagnosis insufficient and not substantiated by illustrated specimens

Rugidinium undulatum
Holotype (reoriented)



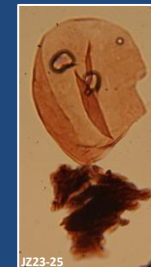
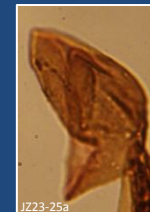
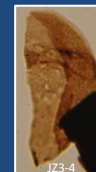
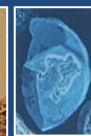
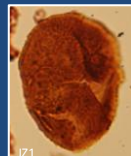
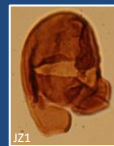
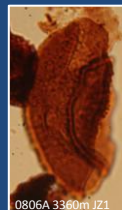
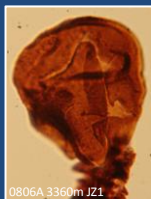
Rugidinium ornatum
(reoriented)

Diagnosis (from Pocock & Sarjeant 1972)
“Vesicle ovoid to subspherical, dividing into three dissimilar sections. Two of these sections represent the main part of the vesicle, the third (and the smallest) forming the apical cap. Wall two-layered, the outer layer rugulose, giving the surface an overall undulose appearance. Other ornament, when present, comprises narrow anastomosing ridges, more or less paralleling the margins of the two portions forming the main part of the vesicle”.

No trilete

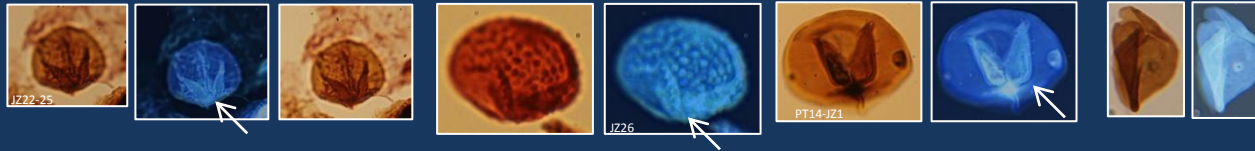


Rugidinium ornatum, from Fig.1 in Pocock & Sarjeant 1971. The drawings are rotated 180 degrees. Original caption reads; “a and b; larger (left) and smaller (right) sections of the main body of the vesicle”. The third specimen, c, is captioned; “Complete main body, lacking only the apical cap”. Sub polar concavity visible in 3, undulose margin in 2.
Note. In the original publication the diagrams are labelled 1-3, but the caption is a-c.



Rugidinium spp. from Late Triassic and Jurassic, NNS

Immature ARC in the early stages of growth. "Butterfly"

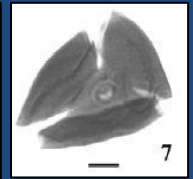
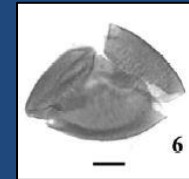


"Loose tetrad". Illustrated specimen of Richardson 1988, Pl.19, fig. 8. Late Ordovician-Early Silurian.

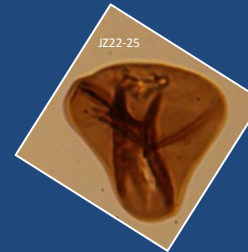
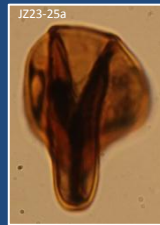


Sangarella lenaensis
Early Cretaceous

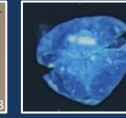
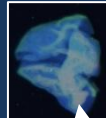
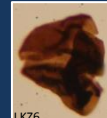
from Pestchevitskaya & Fradkina 2001



Spore Type 1 in Shushang Hu 2006, Pl. 22, figs 6 & 7; "spores tetrahedral trilete(?), laesurae not clear because of splitting, hilate in distal view". Cenomanian.



500μ

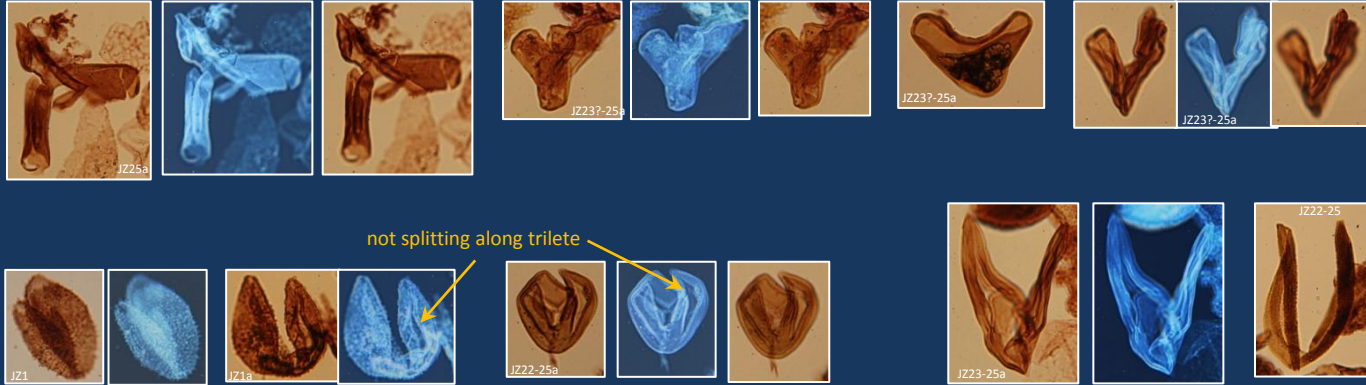


3 sections, approximately equal in size

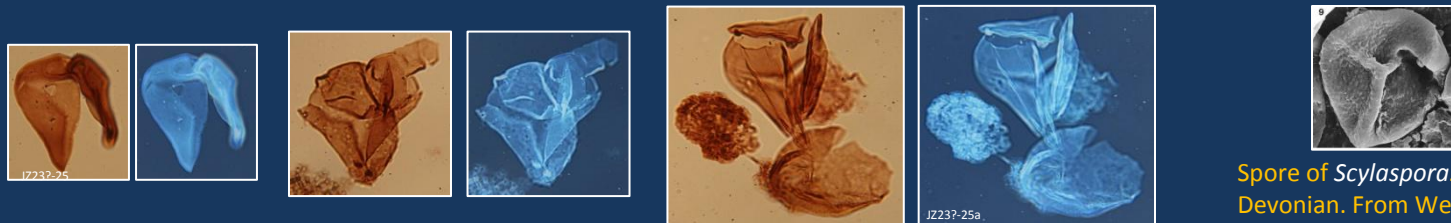
↘ = triple junction

Isolated sections of *Teichertodinium*

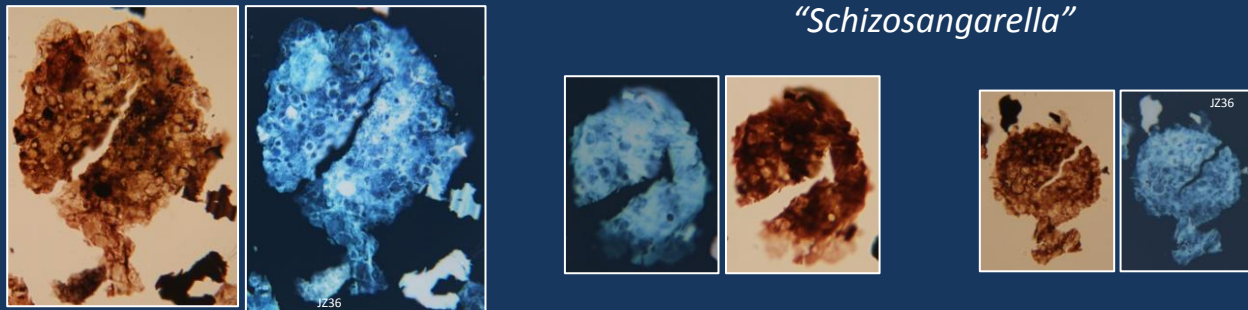
Other varieties of spore-like attached reproductive cells



cf. Teichertodinium: splits but remains intact. Trilete mark present on lateral surface.



"Schizosangarella"



Attached reproductive cells may be gamete-producing antheridia

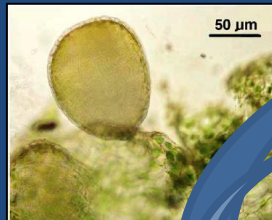
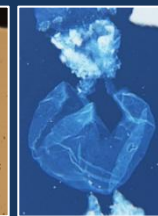
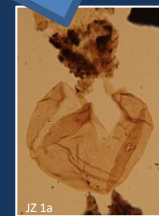
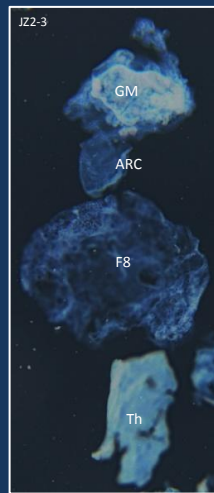
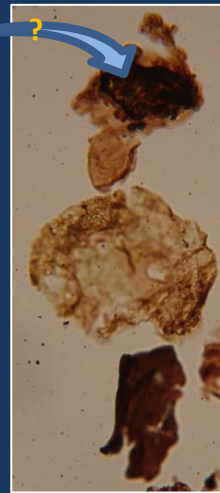


Figure 21. Antheridia of a hornwort. Photo by Hatice Ozenoglu Kiremit.



Figure 22. Antheridia of a hornwort dispersing its sperm. Photo by Hatice Ozenoglu Kiremit.

From Glime et al. 2013

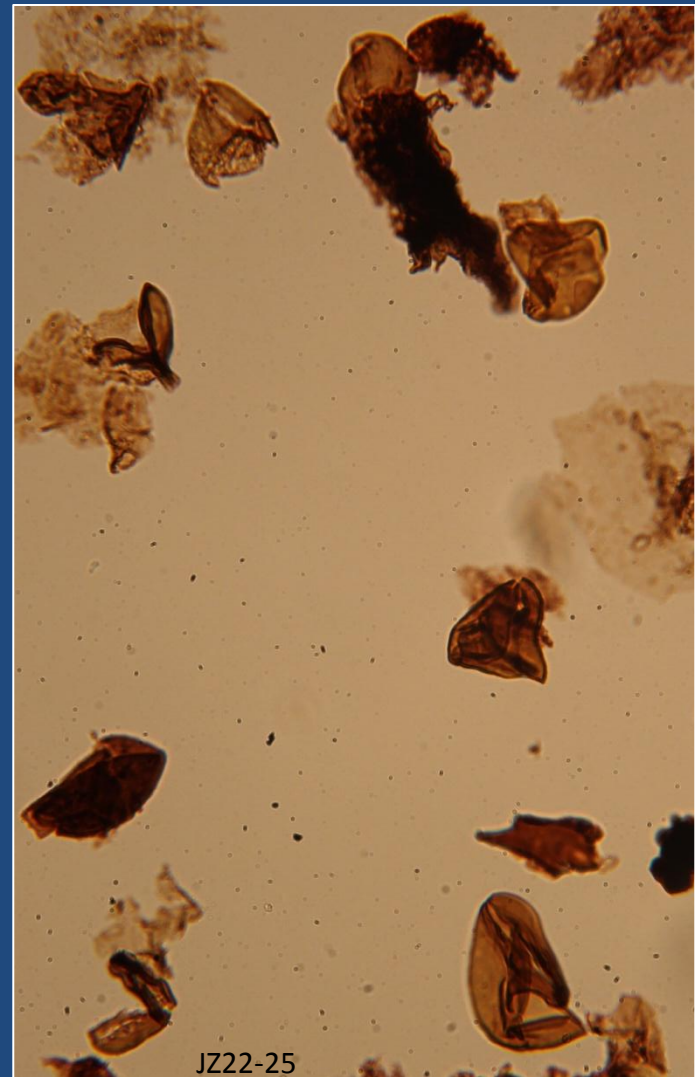
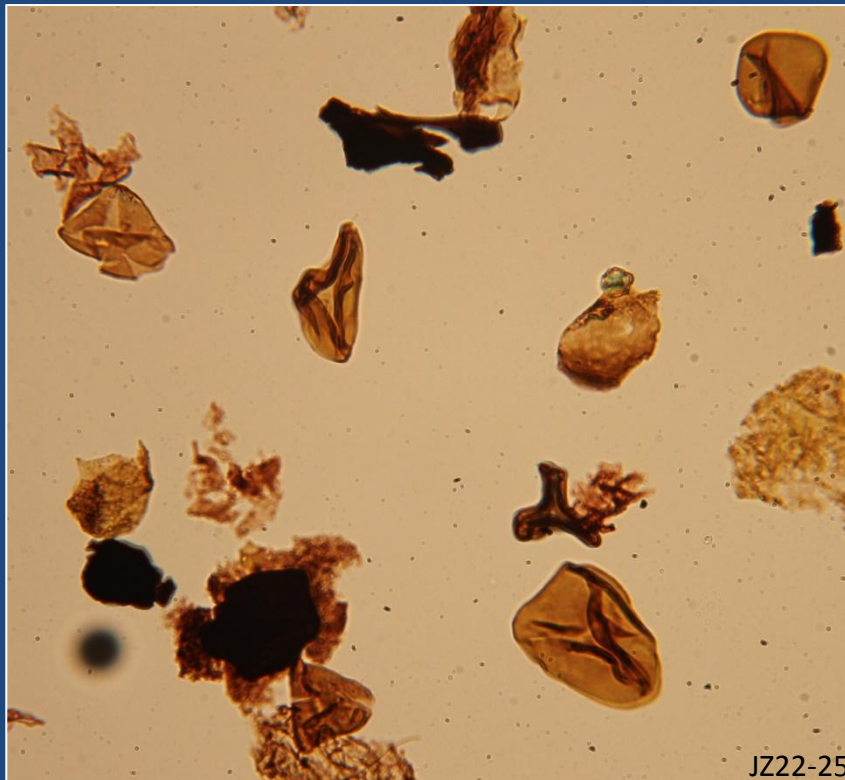


ARC Attached reproductive cell
F8 F8 cell
Th Thalloid cell
GM Gamete mass?

500 μ

Attached reproductive cells are abundant, diverse and widespread. With a very few exceptions, they have been completely overlooked.

Emendation of term "miospore"?
ARCs already published as spores.

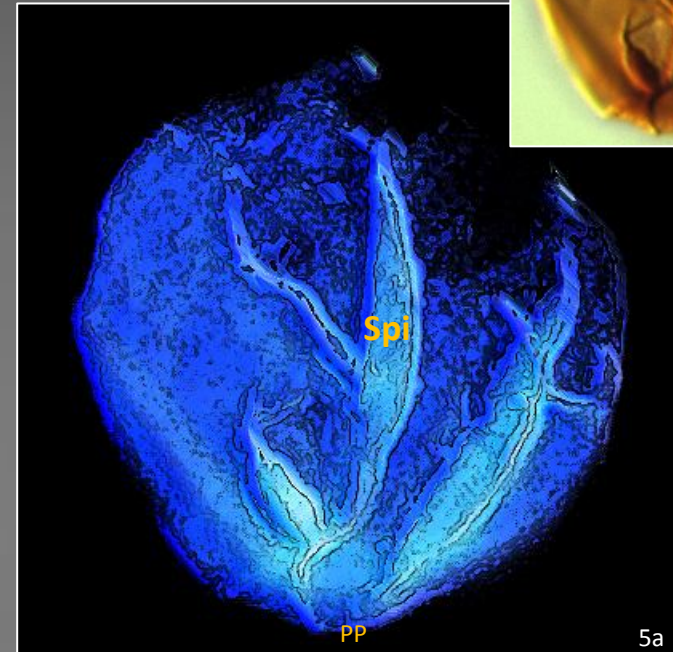


500μ

"Microfolium"

Microfolium: - A "protophyte" within some miospores and acritarchs, arising from the proximal pole as branch-like elements. The microfolium exhibits growth within the expanding host cell, initially as a minute butterfly shaped structure centred on the proximal pole (1 & 2). Growth habit varies, but a common pattern is with two larger (lateral), and one smaller (central) branchlet (3). Branchlets may develop a blade-like feature similar to a spear tip (spiculum) distally (5). Some microfolia appear to "outgrow" the cell and bend sharply inwards across the distal portion of the cell (4). In most cases, the branchlets appear to be fused into the cell wall. Smaller side branches may be observed arising from primary branches (5).

Many miospores and leiosphaerid acritarchs are microfoliate, but this feature has been overlooked, or misinterpreted as folds, kyrtomes, margos and Interadial crassitudes in spores, and as folds in leiospheres.

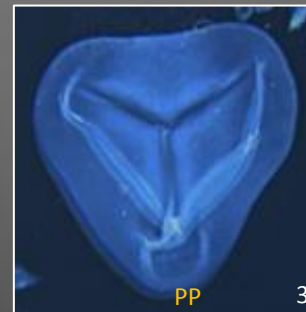
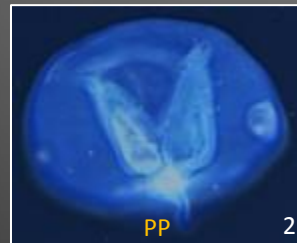


Leiosphaeridia sp., Late Cambrian. Note the secondary branching of the microfolium and **distolateral** rupturing of the cell.



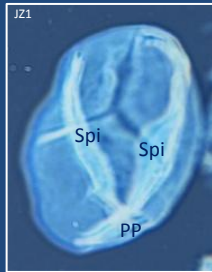
5b

voluminella

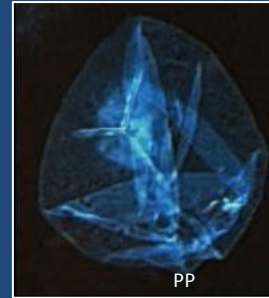


1-4, Attached reproductive cells, illustrating cell growth and stages in the growth of the microfolium (Triassic-Jurassic, NNS).

Microfoliate miospores



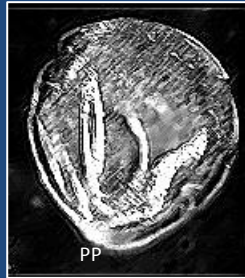
Todisporites sp. Are Formation, Hettangian, Mid Norway. Two longer and one short branchlets. Trilete on lateral surface?



Calamospora impexa. Triassic. From Vigran *et al.* 2014, Fig. 26.B (reoriented). Specimen illustrates secondary branching of the microfolium.



Aratrisporites cf. *minimus*. Are Formation, Hettangian, Mid Norway. Growth of the microfolium primarily axial.



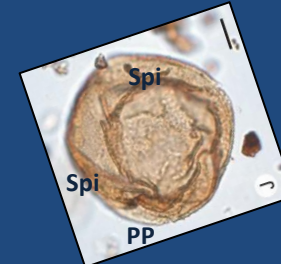
Classopollis chateunovi Reyre 1970. Illustrated specimen of Mildenhall 1994 (reoriented). From Raine *et al.* 2011.



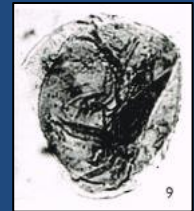
Dictyophyllidites harrisii. Illustrated specimen from the Type Material of Couper, 1958, pl.21, fig.5. Middle Jurassic.



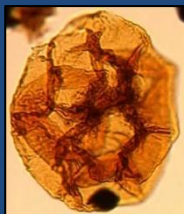
Geminospora sp. A *sensu* Wicander & Playford 2013, Plate 5, fig. 20 (reoriented). Late Devonian, Illinois.



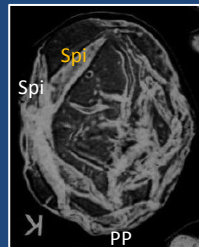
Araucariacites cf. *australis*. Illustrated specimen of Cantrill & Raine 2006 (reoriented). Taken from Raine *et al.* 2011. E. Jurassic.



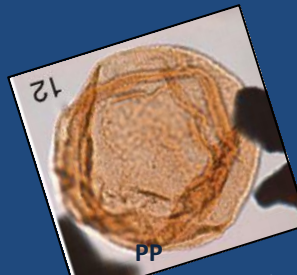
Perinopollenites elatoides Holotype from Couper 1958 pl. 27, fig.9. Mid Jurassic.



Laricoidites subcarpaticus, polar view. Late Triassic of the Barents Sea



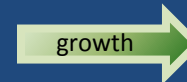
Inaperturopollenites readi. From Zhang & Grant-Mackie 2001, Fig. 24.K (reoriented)



Araucariacites australis. Illustrated specimen of Bonis 1983 Pl. 1, Fig. 12 (reoriented). Triassic-Jurassic transition.



Inaperturopollenites dubius. Illustrated specimen of Norris 1969, Pl. 110, fig 9 (reoriented).

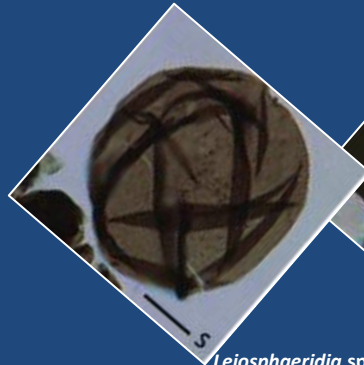


Araucariacites australis. Illustrated specimen of Norris 1969 Pl. 110, fig. 17 (reoriented).

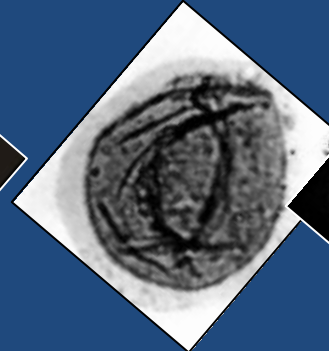
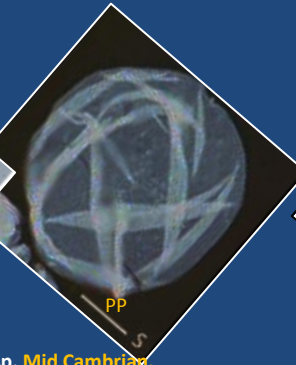
scales vary

Microfoliate acritarchs

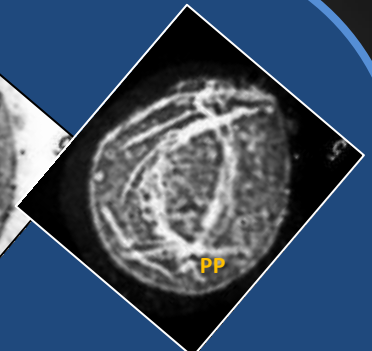
Attached reproductive cells?



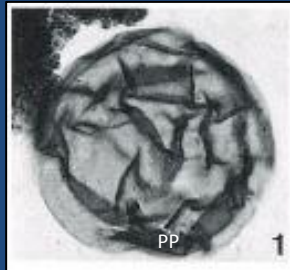
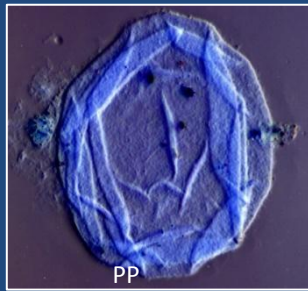
Leiosphaeridia sp. Mid Cambrian.
Illustrated specimen of Traverse 2007, pl 6.1 fig. S (reoriented).



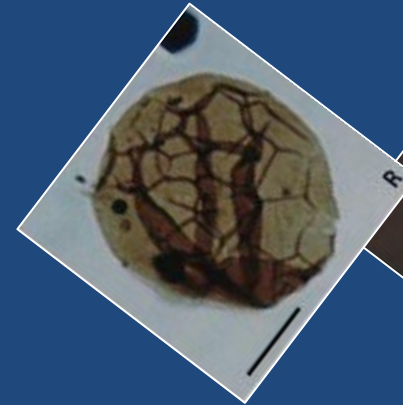
"Marine cyst". Pl 27, fig. 5 in Pocock 1970 (reoriented) Jurassic.



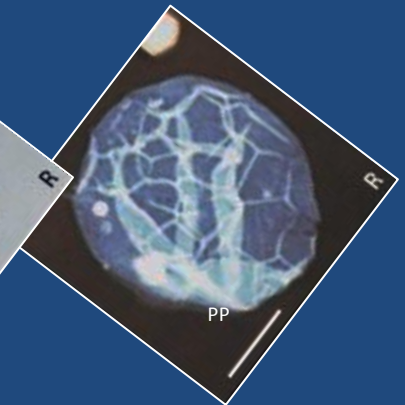
Comasphaeridium molliculum From Moczydlowska and Vidal 1988. (1521-22) at www.fossilid.info University of Talin (reoriented).



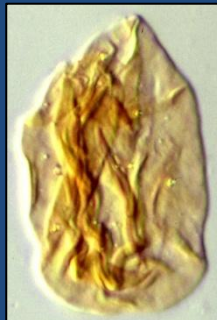
Leiosphaeridia asperata
From Baudet 1988, Pl.2, fig.1. Precambrian, Libya.



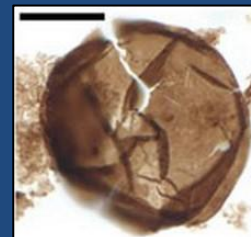
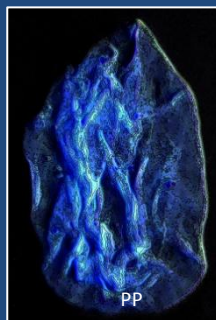
Retisphaeridium dichamerum Staplin et al. Middle Cambrian. Illustrated specimen of Traverse 2007, pl. 6.1 fig. R (reoriented). Three primary branchlets.



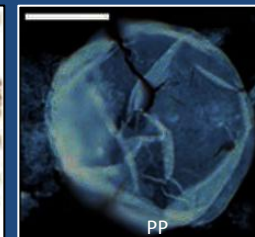
scales vary



Leiosphaeridia gregalis Hagenfeldt 1989. Middle Cambrian. Illustrated specimen (1521-12) from www.fossilid.info. University of Talin (reoriented).



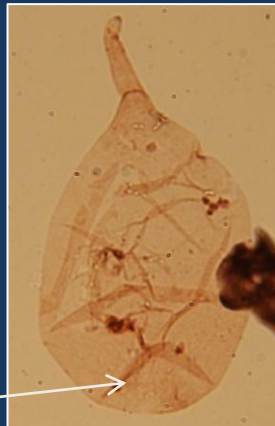
Valeria lophostriata. Illustrated specimen of Nagy et al. 2009, Figure 1.a



Folding vs. microfolium

Pareodinia ceratophora, Jurassic dinocyst. Thin-walled, compressed specimen with numerous folds.

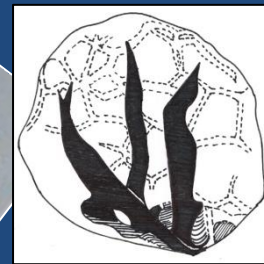
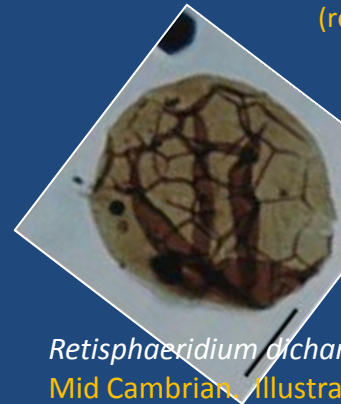
- No “plant-like” appearance.
- No point of convergence (PP).
- More or less uniform distribution.
- Widest in middle, pointed both ends.
- Often crossing.
- “Boomerangs” – darker mid section.



Still at an early stage, but already clear that microfolia exhibit numerous and different growth habits. These are likely to be high level criteria for systematics & taxonomy.



Inaperturopollenites dubius.
Illustrated specimen
of Norris 1969, Pl. 110, fig 9
(reoriented).

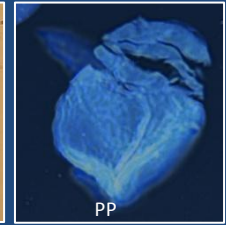
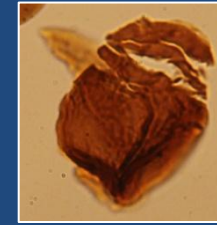
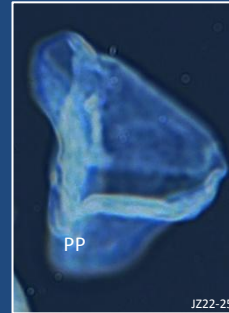
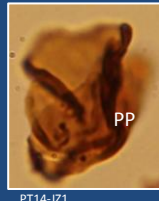
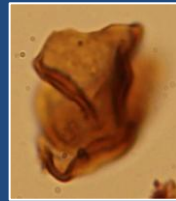


Retisphaeridium dichamerum Staplin et al.
Mid Cambrian. Illustrated specimen of
Traverse 2007, pl. 6.1 fig. R (reoriented).
Three primary branchlets.



Leiosphaeridia sp. Late Cambrian, Ulgase
Formation, Estonia. Illustrated specimen
(1520-19) from www.fossilid.info
University of Talin (reoriented).

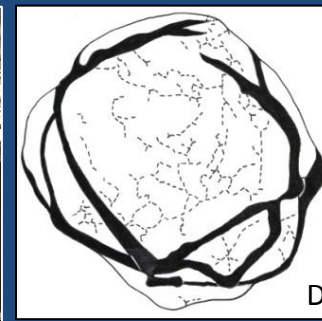
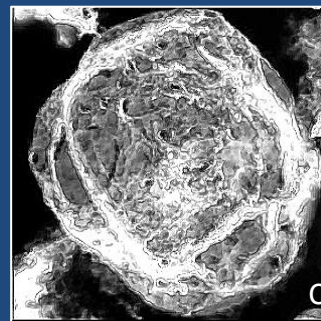
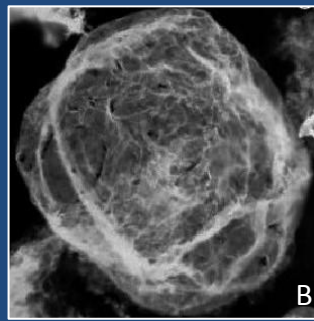
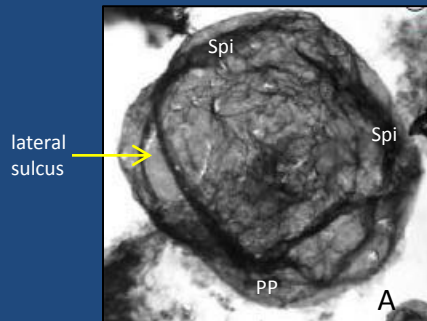
Microfolium: dehiscence mechanism?



?*Teichertodinium* spp. Note how branchlets of the microfolium are fused into the cell wall

Dehiscence is the splitting of the cell wall at maturity along built-in line of weakness, usually facilitated by drying.

Stress might be produced by differing desiccation rates of the cell wall and the thicker branchlets. There may also be elastic energy stored in the curved branchlets.



Leiosphaeridia sp. Cuneiform (wedge-shaped) acritarch from the Australian Mesoproterozoic. Figure 2g in: Knoll *et al.* 2006 (reoriented). The microfolium comprises four branchlets, two on each side. The depression between each pair forms a lateral sulcus, which is wider proximally, becoming narrower distally. A, original image. B & C, inverted images with different contrast. D, line drawing with interpretation of microfolium E, schematic interpretation PP = proximal pole. Spi = spiculum.

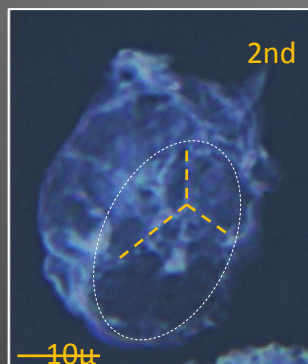
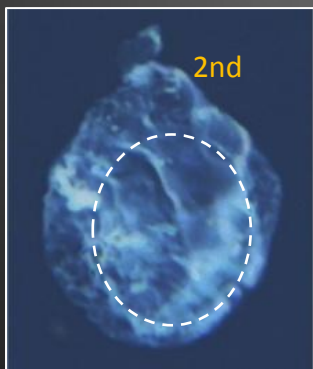
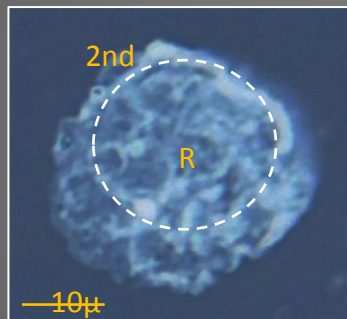
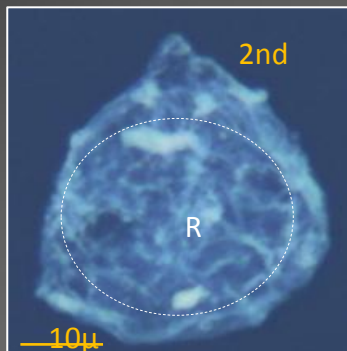
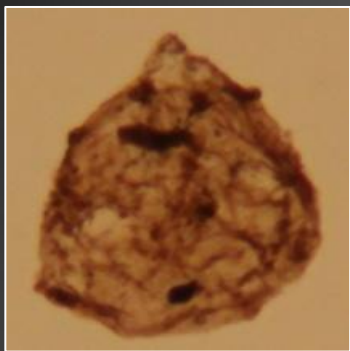
There are even more types of reproductive cell...



“Sangarelladinium”



"Sangarelladinium"



- Sub triangular to sub pentagonal, often lacrimate (teardrop) in outline. Lenticular or flattened in cross-section.
- Normally alete, sometimes indistinctly trilete.
- Curvatural thickening, with or without "rosette".
- Primary horn (polar) & secondary horn (sub polar).
- Clusters/polyads, ?diads, isolated or in short chains.
- Linkage of cells may be polar, sub-polar or lateral.
- Lateral sulcus (variable).
- Microfoliate

These features are variable
from obvious to absent!

2nd - secondary horn; incipient to prominent

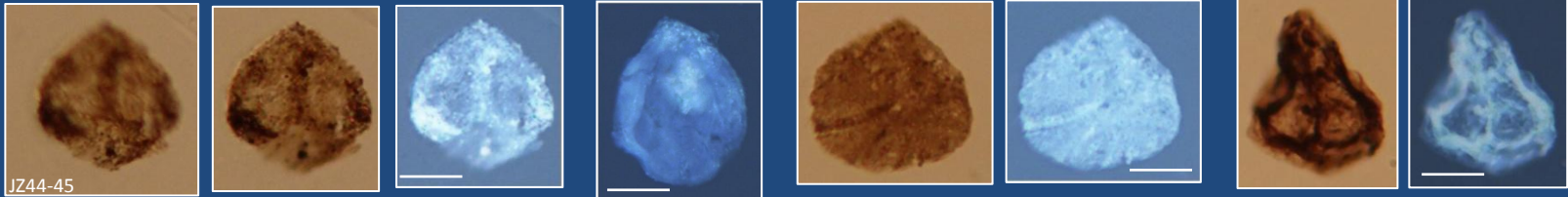
 - curvatural thickening

R - "rosette"

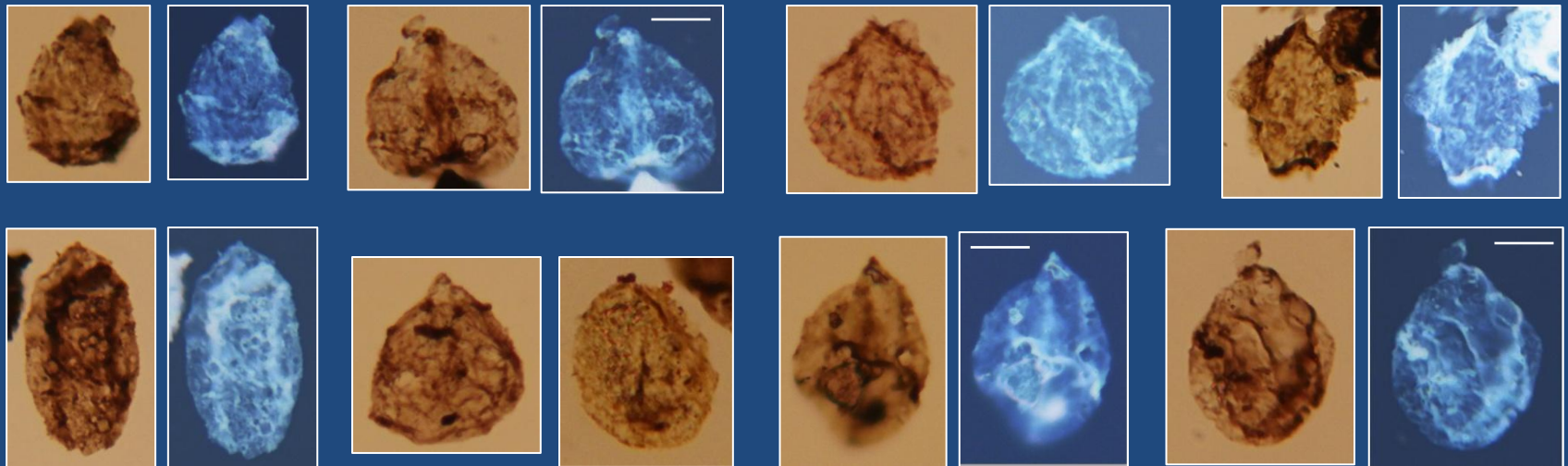
 - trilete mark

Affinity of “*Sangarelladinium*”?

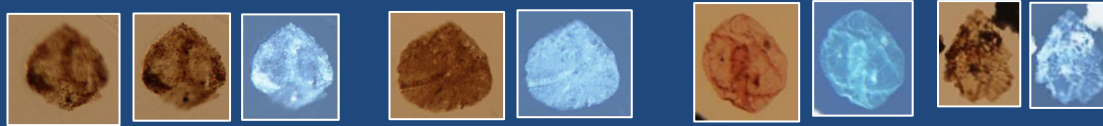
Spore-like



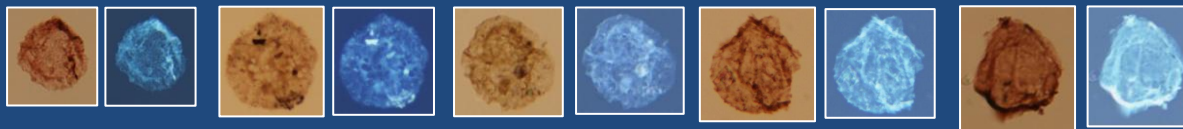
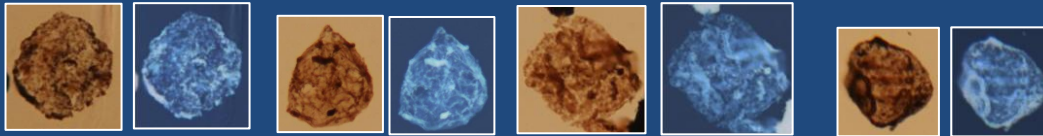
Dinocyst-like



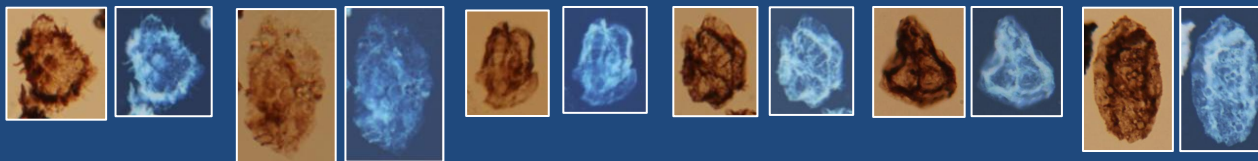
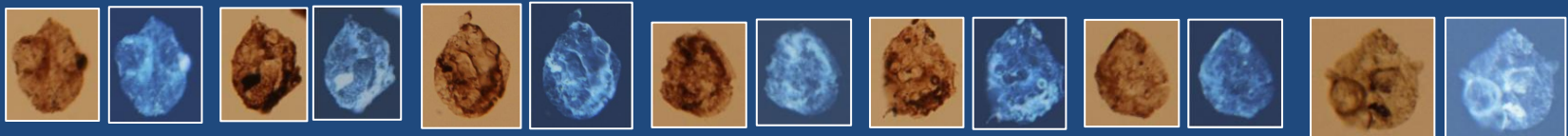
"Sangarelladinium" is abundant and ?ubiquitous



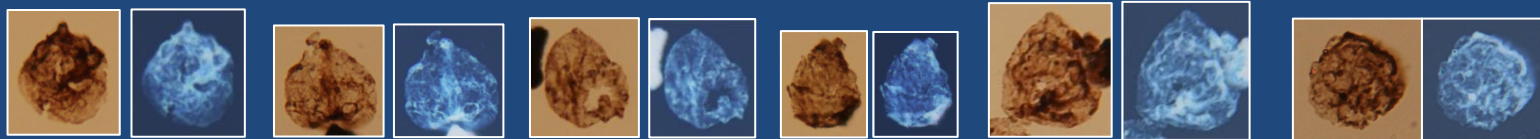
Tithonian NNS



Kimmeridgian NNS



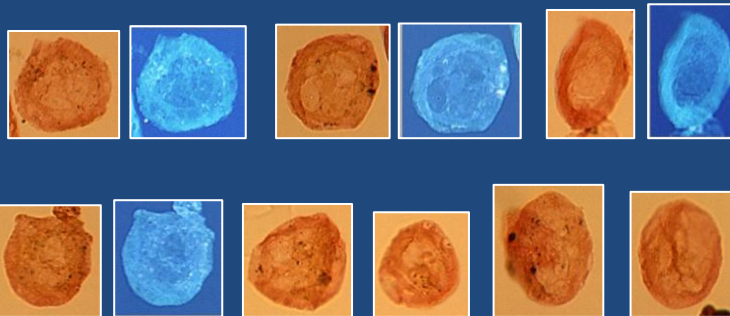
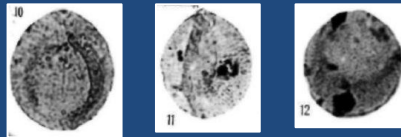
Oxfordian NNS



Also abundant, locally dominant throughout the Late Triassic to Jurassic (at least)

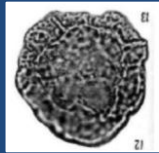
"Sangarelladinium" has probably already been published from the Jurassic of northern Canada

Leiosphaeridia granulosa Pocock 1972

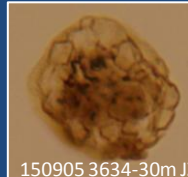


Originally logged as *Lecaniella* sp. 6. NNS JZ42-43 Early Tithonian

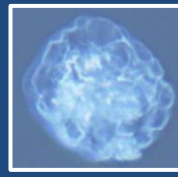
Pterospermopsis bulbosum Pocock 1972



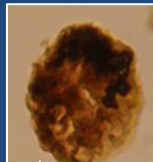
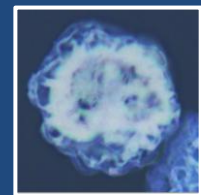
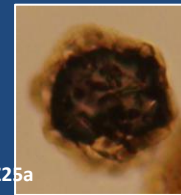
Holotype, Pocock 1972
(reoriented)



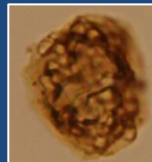
150905 3634-30m JZ25a



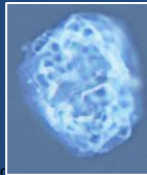
150905 3634-30m JZ25a



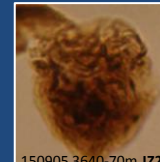
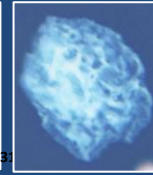
15/9-5 3617-40m JZ25



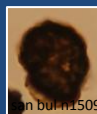
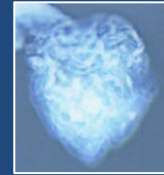
150905 3634-30m x40 JZ25



1503A1272 5925m JZ31



150905 3640-70m JZ25



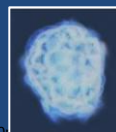
150907 3616-30m x40 JZ25



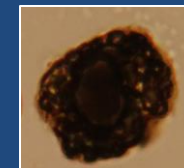
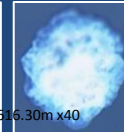
150980412 6198.5m JZ25a



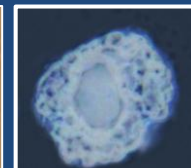
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150907 3616-30m x40 JZ25

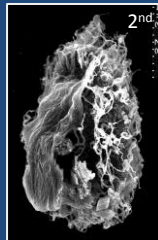


15/9-5 3555.10m JZ25

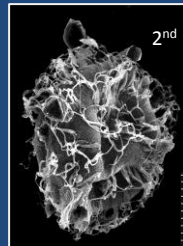
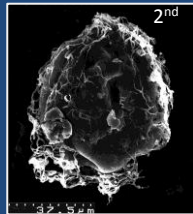


"*Sangarelladinium bulbosum*" Middle Jurassic

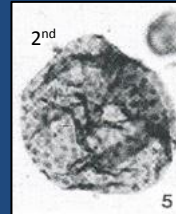
Palaeozoic & Precambrian Acritarchs with “*Sangarelladinium*” – like features



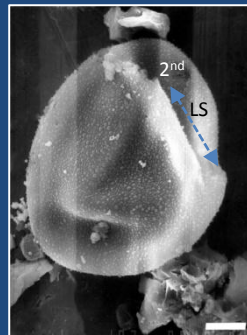
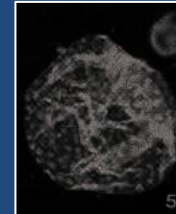
Aryballomorpha sp. Leetse Formation, ?Tremadocian of Estonia. Note flattened ?proximal surfaces with reduced ornament and sub polar secondary horns.



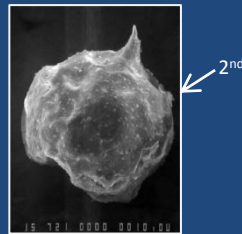
Aryballomorpha grootaertii Martin & Leiming 1988, ?Tremadocian of Estonia



Kildinosphaera verrucata. Illustrated specimen of Knoll, 1996, pl.4, fig.5. Pre-Cambrian.



Lophosphaeridium disparpelliculum Playford & Martin 1984. Ordovician, Rapla Borehole, Estonia. Note lateral sulcus and secondary horn.



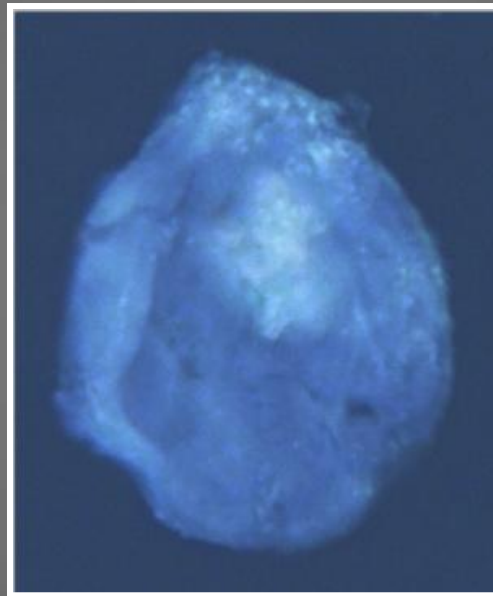
Bacisphaeridium granulatum Uutela & Tynni 1991. Late Ordovician, Estonia. Clearly defined secondary horn



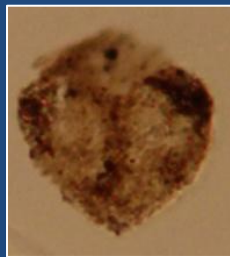
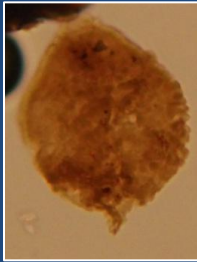
Leiosphaeridia? voigtii Eisenack 1958 Tremadocian, Estonia. Discoidal, with “rosette” visible on facing surface.

Unless indicated, all from www.fossilid.info

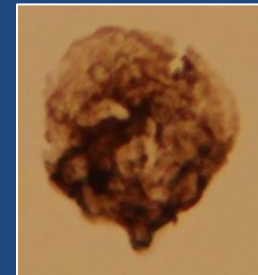
So what is *Sangarelladinium*?



**Gemma of extant
liverwort *Marchantia***



50μ approx



***"Sangarelladinium confusum"*
from the Mid-Late Jurassic**

Gemmae: asexual propagules of bryophytes.

Minute clones propagate by vegetative growth.

Primitive kind of dispersed spore

Gemmae cups and gemmae of extant liverwort *Marchantia*.



1mm approx for gemmae cups

Gemmae cups, - a primitive type of “open sporangium”

Gemmae cups of the liverwort *Marchantia polymorpha*



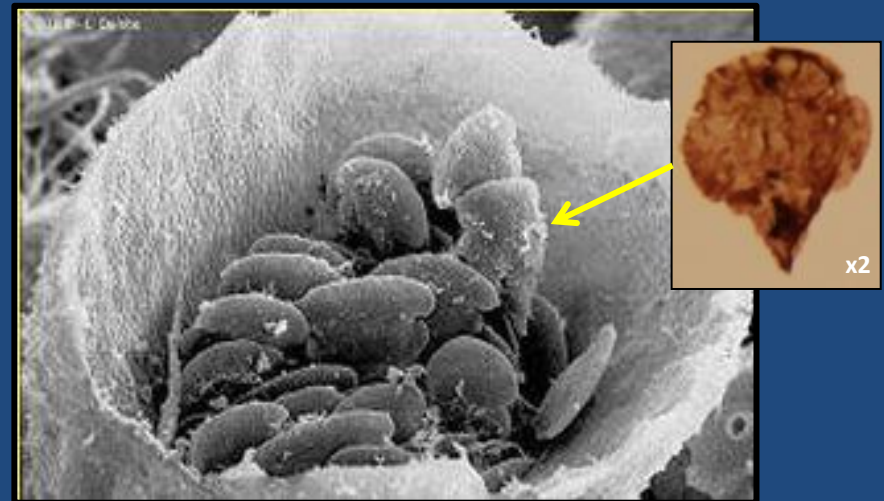
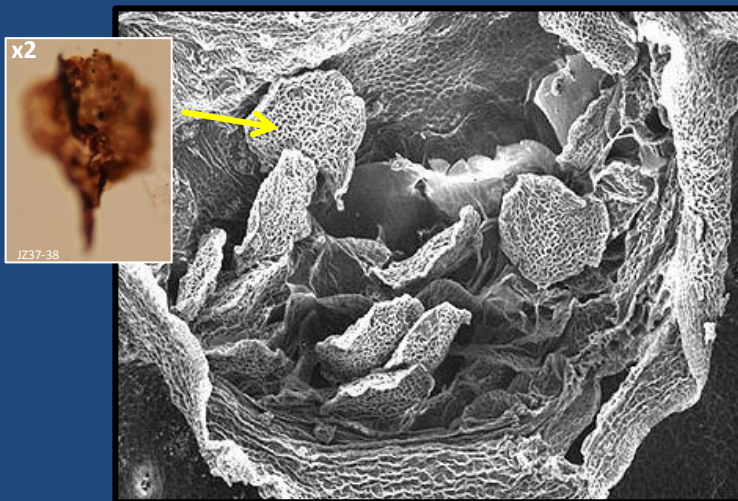
Lens-shaped

Dispersal by raindrops

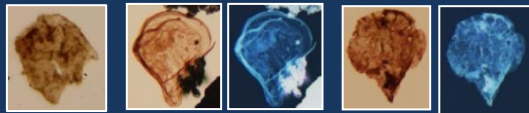
Gemmae cups and gemmae

Gemmae cup of *Lunularia cruciata*, an extant liverwort. www.botany.ubc.ca

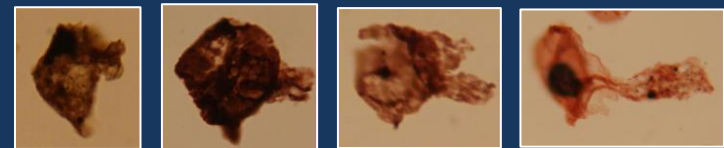
Liverwort gemmae in gemmae cup. www.ou.edu



500 μ approx



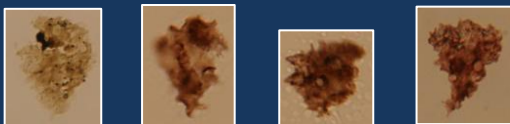
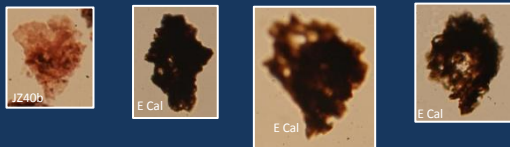
Early Jurassic, Mid Norway



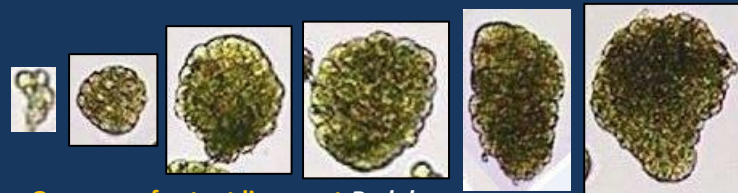
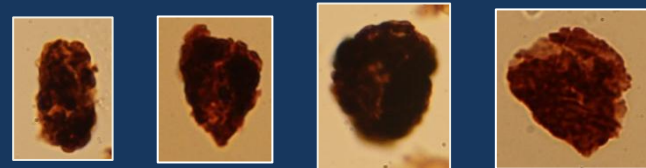
Early vegetative growth of Jurassic gemmae

Modern and fossil gemmae

"Sangarelladinium" sp. D
Heather Fm. (Late Oxfordian)



"Sangarelladinium asperum" Åre Formation (Hettangian)

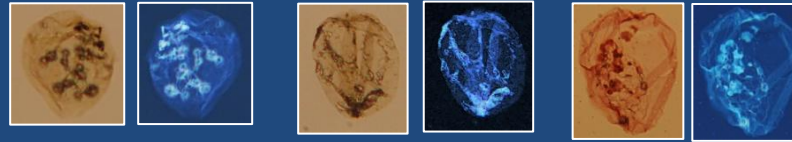


Gemmae of extant liverwort *Radula*
www.una.edu

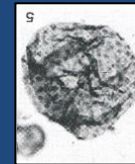
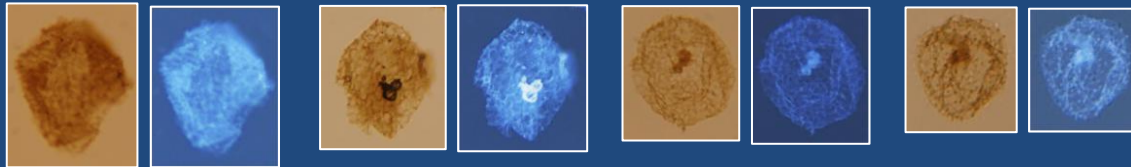


"Sangarelladinium asperum" Hugin & Sleipner Fm, Callovian

"Sangarelladinium ignotum" very abundant in Hugin

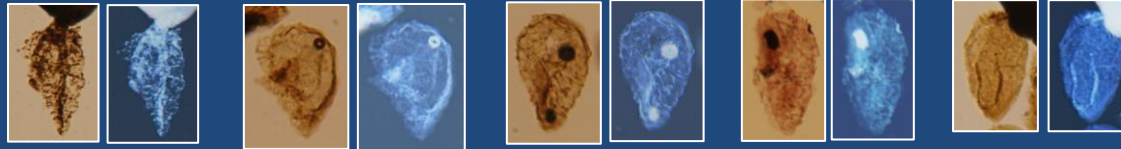


"Sangarelladinium reticulata" common in Callovian

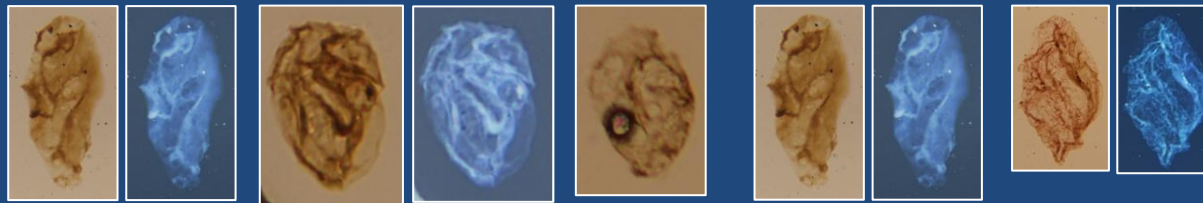


Kildinosphaera verrucata.
Illustrated specimen of
Knoll, 1996, pl.4, fig.5.
Precambrian (reoriented).

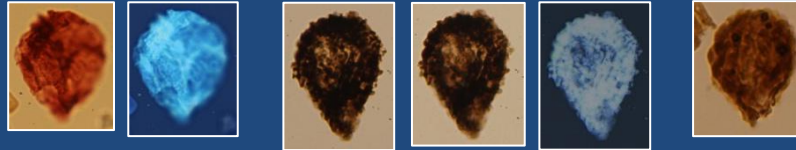
"Sangarelladinium reticulata" ssp. Callovian



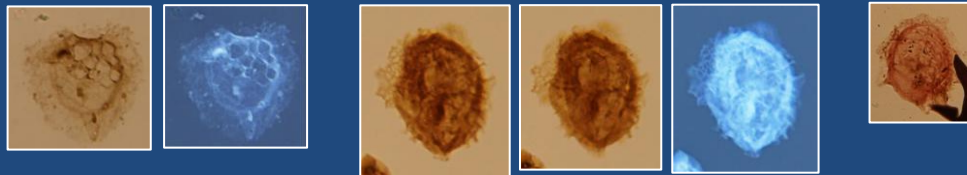
"Sangarelladinium elongatum" Early-Middle Jurassic



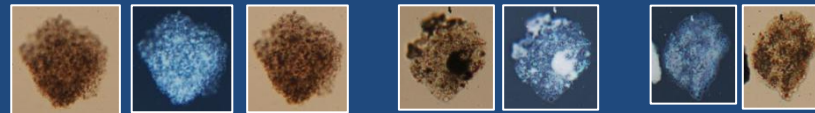
"Sangarelladinium asperum" Triassic-Jurassic?



"Sangarelladinium magnificum" Callovian



"Sangarelladinium" sp. M Early Callovian



"Sangarelladinium" sp. K Callovian-Kimmeridgian



Gemmae and other vegetative propagules of hepatic plants are abundant in the fossil record and probably ubiquitous in palynological samples from sediments of Mid Ordovician age and younger .

Many have already been published as spores, cryptospores, pollen, dinocysts and acritarchs.

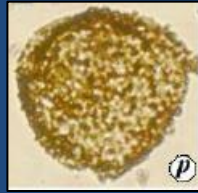
Small selection of species and illustrated specimens

List of references available at BioStrat.org.uk/taxonomy

Gemmae published as spores, cryptospores or pollen (all reoriented)



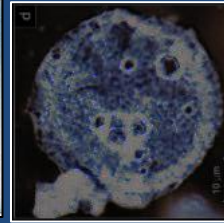
Lundbladispora brevicula
sensu Awatar *et al.* 2014
(Figure 4a). Permian.



Cyclogranisporites distinctus
sensu Awatar *et al.* 2014 ,
(Figure 4d) Permian



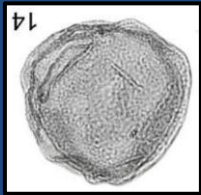
Hispanaediscus sp.B. Illustrated
specimen of Steemans *et al.*, 2000,
pl.2, fig.d. Llandovery.



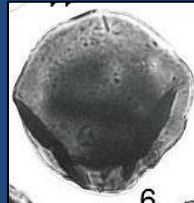
Laevolancis chibrikovae
Illustrated specimen of
Steemans *et al.*, 2000,
pl.2, fig.n. Llandovery.



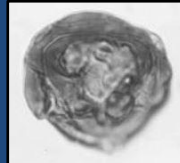
?*Retialetes* sp. Illustrated
specimen of Le Hérissé *et al.* 2001, Plate 2, fig. 8.



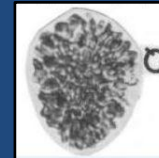
Araucariacites punctus.
Pl. 6, fig 14, in Cornet &
Traverse 1975



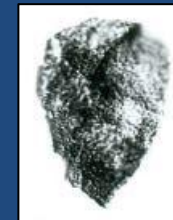
Pilasporites allenii.
Illustrated specimen
of Cornet & Traverse
1975 , pl. 4, fig 11.



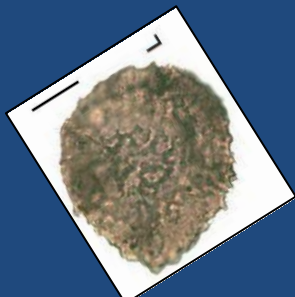
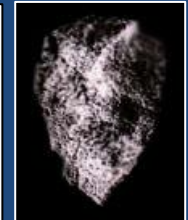
Discisporites psilatus
Plate 12, figure A, in
de Jersey & Raine 1990



Thymospora ipsviciensis
Figure 22Q in Zhang and
Grant Mackie 2001



Microfoveolatispora sp. *sensu*
Abu Hamad 2004, Pl.32, Fig 1



Convolutispora subtilis.
Illustrated specimen of
Noetinger & Di Pasquo, 2011,
fig II L. Devonian, Argentina.



Discisporites verrucosus
From de Jersey & Raine
1990, pl. 3, fig. J. Triassic
(possible).



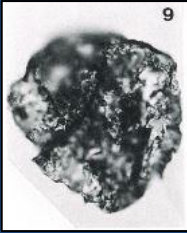
Secarisporites lacunatus.
Illustrated specimen of
Backhouse 1988, fig.16 G.
Permian.



Triadispora obscura. Illustrated specimen
of Vigren *et al.* 2014, Pl.10, S. Middle
Triassic, Svalbard (possible).



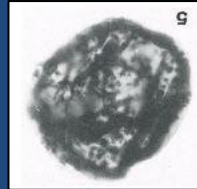
Published as acritarchs, including pre-embryophytic. All reoriented



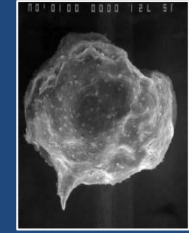
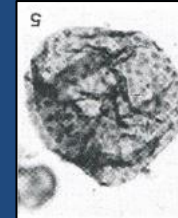
Sphaeromorph sp. Illustrated specimen of Baudet 1988, Pl.3, fig.6. Precambrian, Libya.



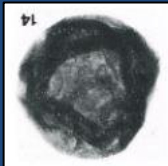
Kildinosphaera verrucata. Illustrated specimen of Baudet 1988, Pl.4, fig.5. Precambrian, NE Libya.



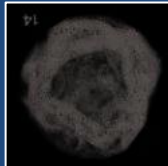
Kildinosphaera verrucata. Illustrated specimen of Knoll, 1996, pl.4, fig.5. Pre-Cambrian.



Bacisphaeridium granulatum Uutela & Tynni 1991. Late Ordovician, Estonia. www.fossilid.info



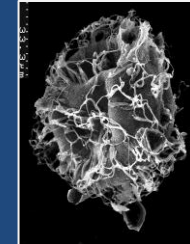
Kildinosphaera chagrinata Illustrated specimen of Baudet 1988, Pl.1, fig.14. Precambrian, NE Libya.



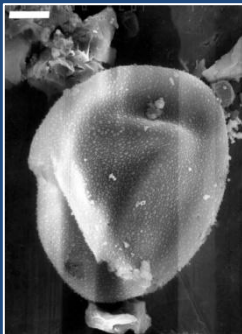
Archaeodiscina sp. Illustrated specimen of Baudet 1988, Pl.3, fig.5. Precambrian, Libya



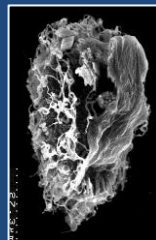
Leiosphaeridia vogtii Eis.1958 Tremadocian, Estonia. www.fossilid.info



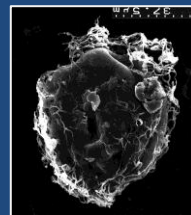
Aryballomorpha grootaertii Martin & Leiming 1988, ?Tremadocian of Estonia www.fossilid.info



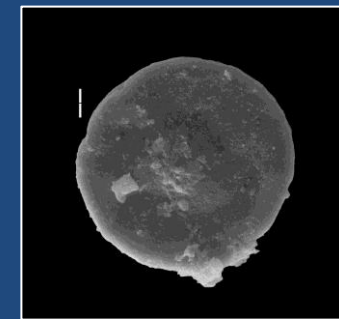
Lophosphaeridium disparpelliculum Playford & Martin 1984. Ordovician of Estonia. Note lateral sulcus and secondary horn. www.fossilid.info



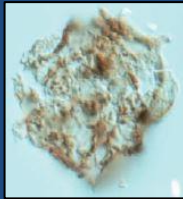
Aryballomorpha sp. Leetse Formation, ?Tremadocian of Estonia. Note flattened ?proximal surfaces with reduced ornament and sub polar secondary horns. www.fossilid.info



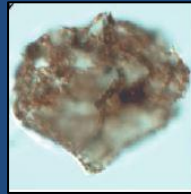
Leiosphaeridia? vogtii Eisenack 1958 Tremadocian, Estonia. Discoidal, with "rosette" visible on facing surface. www.fossilid.info



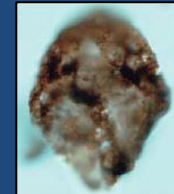
Published as Dinocysts



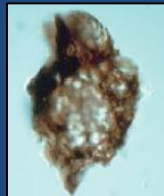
Heibergella cf. salebrosacea
sensu Ghasemi-Nejad *et al.*
2008, Pl. 3, fig. 1 (reoriented).
Late Triassic.



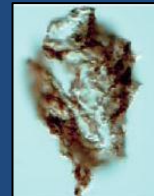
Heibergella cf. salebrosacea
sensu Ghasemi-Nejad *et al.*
2008, Pl. 3, fig. 3 (reoriented).
Late Triassic.



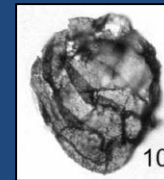
Heibergella sp. *sensu* Ghasemi-
Nejad *et al.* 2008, Pl. 3, fig. 1
(reoriented). Late Triassic.



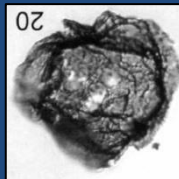
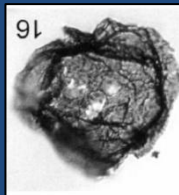
Svedrupiana cf. septentrionalis
sensu Ghasemi-Nejad *et al.* 2008,
Plate 2, fig. 7 (reoriented). Triassic.



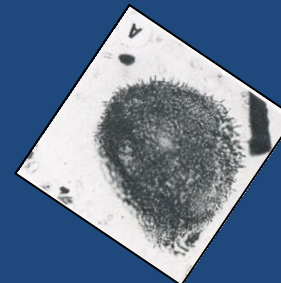
Genus indet. A morphotype 1
sensu Ghasemi-Nejad *et al.*
2008, Pl. 3, fig. 1 (reoriented).
Late Triassic.



cf. Noricysta pannucea sensu
Honchuli & Frank 2000,
Plate 2, figs 16 & 20. Triassic



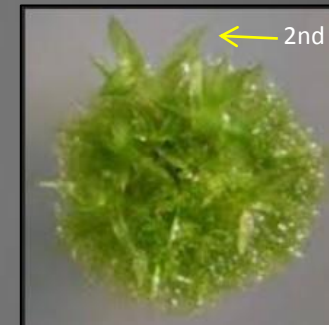
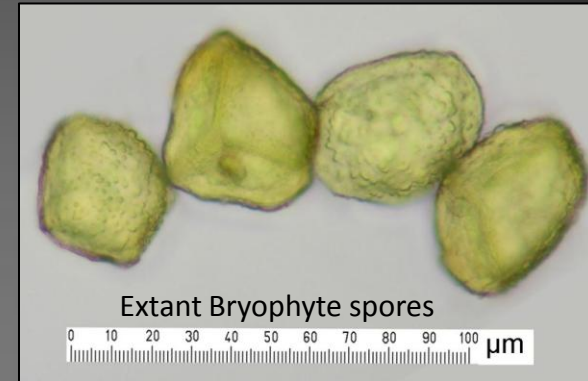
Indeterminate palynomorph , ?dinoflagellate
cysts (37 microns). Illustrated specimen of
Honchuli & Frank 2000, Plate 2, figs 16 & 20



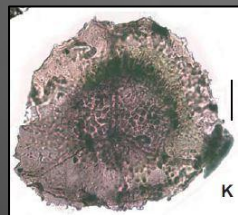
Serjeantia triassica. Illustrated
specimen of Conway & Cousminer
1983, figs. 1A&B . Triassic, Israel.

Hepatic plants may produce gemmae AND dispersed spores

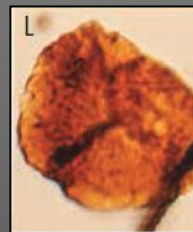
Bryophytic dispersed trilete spores have similar shape to gemmae; lenticular x-section, radial asymmetry & sub polar horn



Samarisporites triangulatus.
Illustrated specimen of
Noetinger & Di Pasquo, 2011,
fig IV C. Devonian, Argentina.



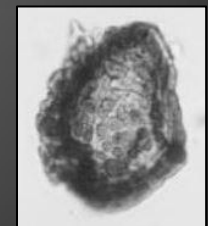
Grandispora protea. From
Noetinger & Di Pasquo, 2011,
fig III K. Devonian, Argentina.



Uvaesporites sp.
Illustrated specimen
of Vigren et al. 2014,
Pl.4, L. Middle Triassic,
Svalbard.



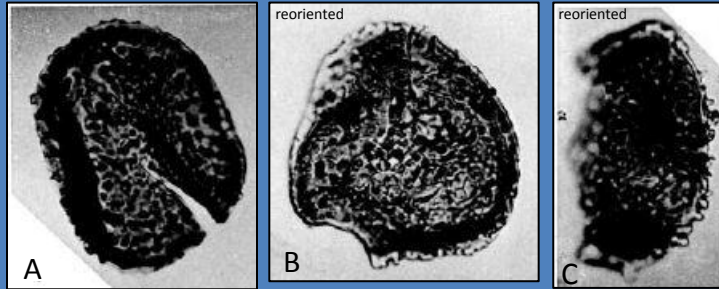
Thomsonisporites undulatus.
Illustrated specimen of
Vigren et al. 2014, Pl.10, I.
Middle Triassic, Svalbard.



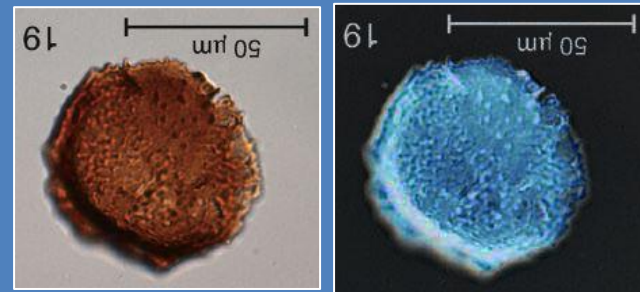
Discisporites verrucosus
From de Jersey & Raine
1990, pl. 3, fig. J. Triassic

Gemma or spore? Does it matter?

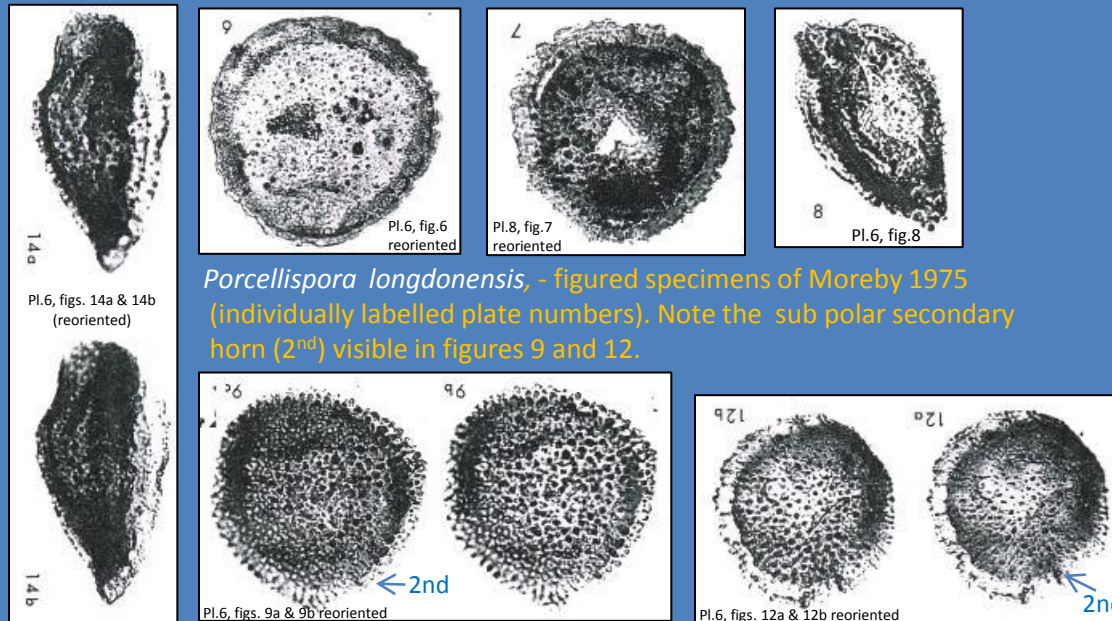
Porcellispora longdonensis (Clark 1965) Scheuring 1970 emend. Moreby 1975



Figured specimens from the type material, including holotype (A). Lateral view (C). From Clark 1965, pl. 36, figs. 1, 3 & 4 respectively.

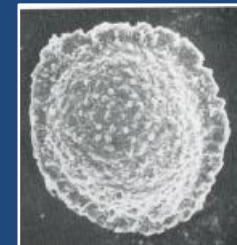


Porcellispora longdonensis. Illustrated specimen of Bonis 1983, pl. II, fig.19 (reoriented). Rhaetian.



Porcellispora longdonensis, - figured specimens of Moreby 1975 (individually labelled plate numbers). Note the sub polar secondary horn (2nd) visible in figures 9 and 12.

Emended diagnosis includes "proximally hilate, occasionally trilete", "zonate or cinguli-zonate", "amb convexly triangular to circular", and "Proximal profile flat to convex, distal profile convex" (Moreby 1975, p. 23).



"Spore of *Naiadita*", a Triassic hepatic. Abundant and well preserved macrofossils, with gemmae cups (gemmae not mentioned). Figure 5.16 in Taylor & Taylor 1993, page 141. "contain spores in tetrahedral tetrads" and "lens shaped"

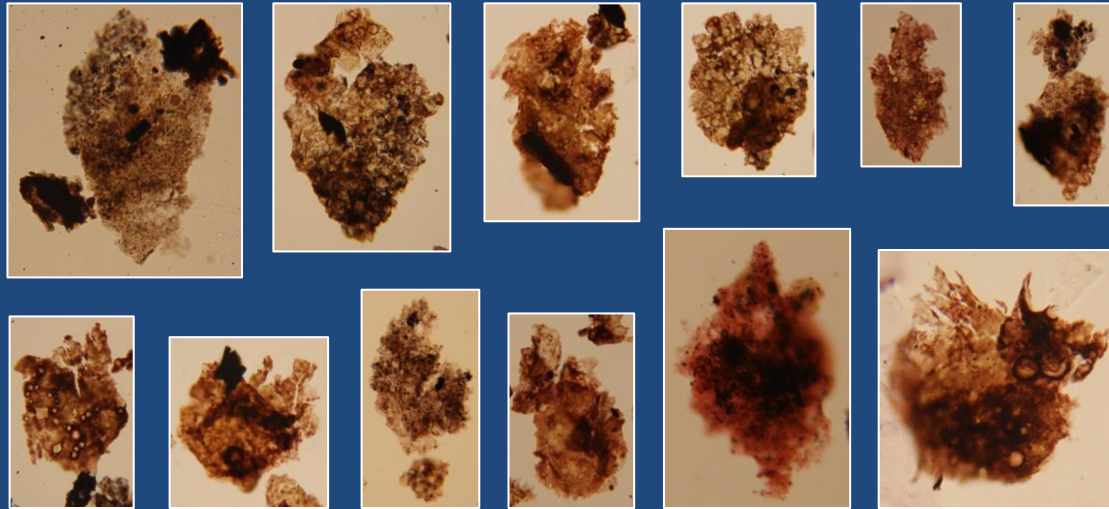
Orientation of hepatic spores?

Caducous vegetative propagula of bryophytes

Bulbils, turions, tubers, leaf buds, adventitious branches, gemmae (pars).

Even randomly broken non-specialised fragments may regenerate.

Hugin-Sleipner Formation (Callovian) SVG



Draupne Formation (Kimmeridgian), SVG

Bulbils?



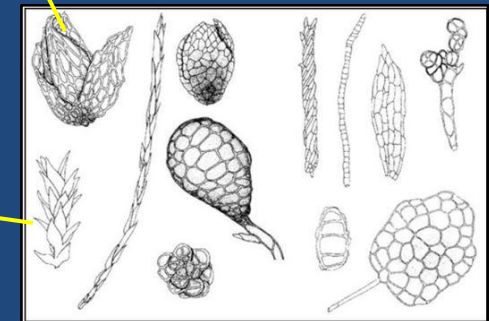
Bryum dichotomum bulbil
from leaf axil Fig 93 in Glime
2014.

Caducous buds?

Late Triassic-Jurassic NNS



500μ



Propagula and gemmae of selected bryophytes.
Figure 74 in Glime 2014 (redrawn from Imura
and Iwatsuki 1990).

All have similar strategy and same outcome as dispersed spores.

Should we include all/some in miospores?

Some already are!

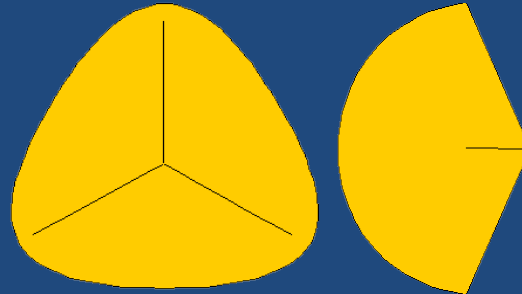
Should “Miospore” be replaced by “Diaspore”?

Glime 2014....“spores and other propagules that function in dispersal”

Diaspores

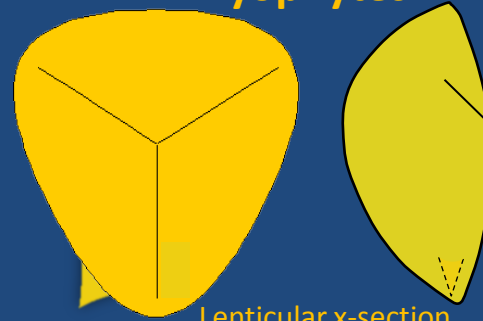
Dispersed

Pteridophytes & Lycophytes



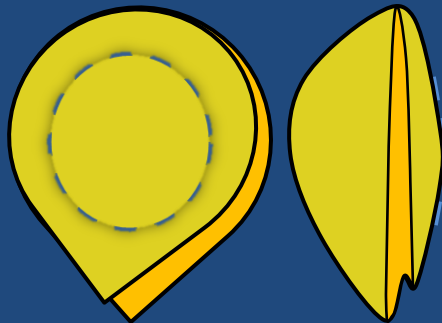
Radial symmetry, trilete

Bryophytes



Lenticular x-section
no radial symmetry, trilete

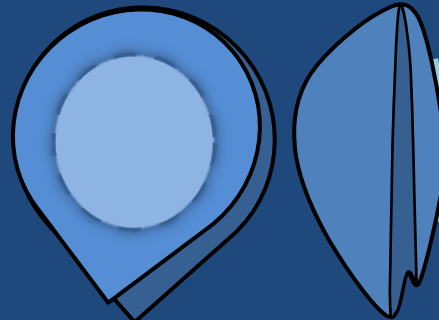
Bryophytes & Cryptospores?



Lenticular: alete/hilate

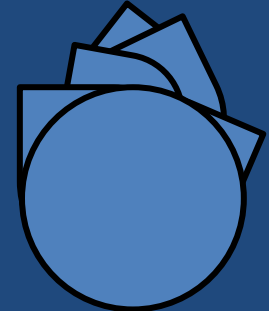
? =

Gemmae



Lenticular: alete/hilate

Bulbils, tubers etc.

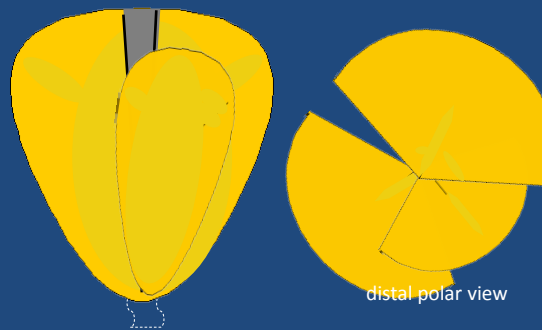


Other vegetative
propagules

Caducous



"Schizosangarella"



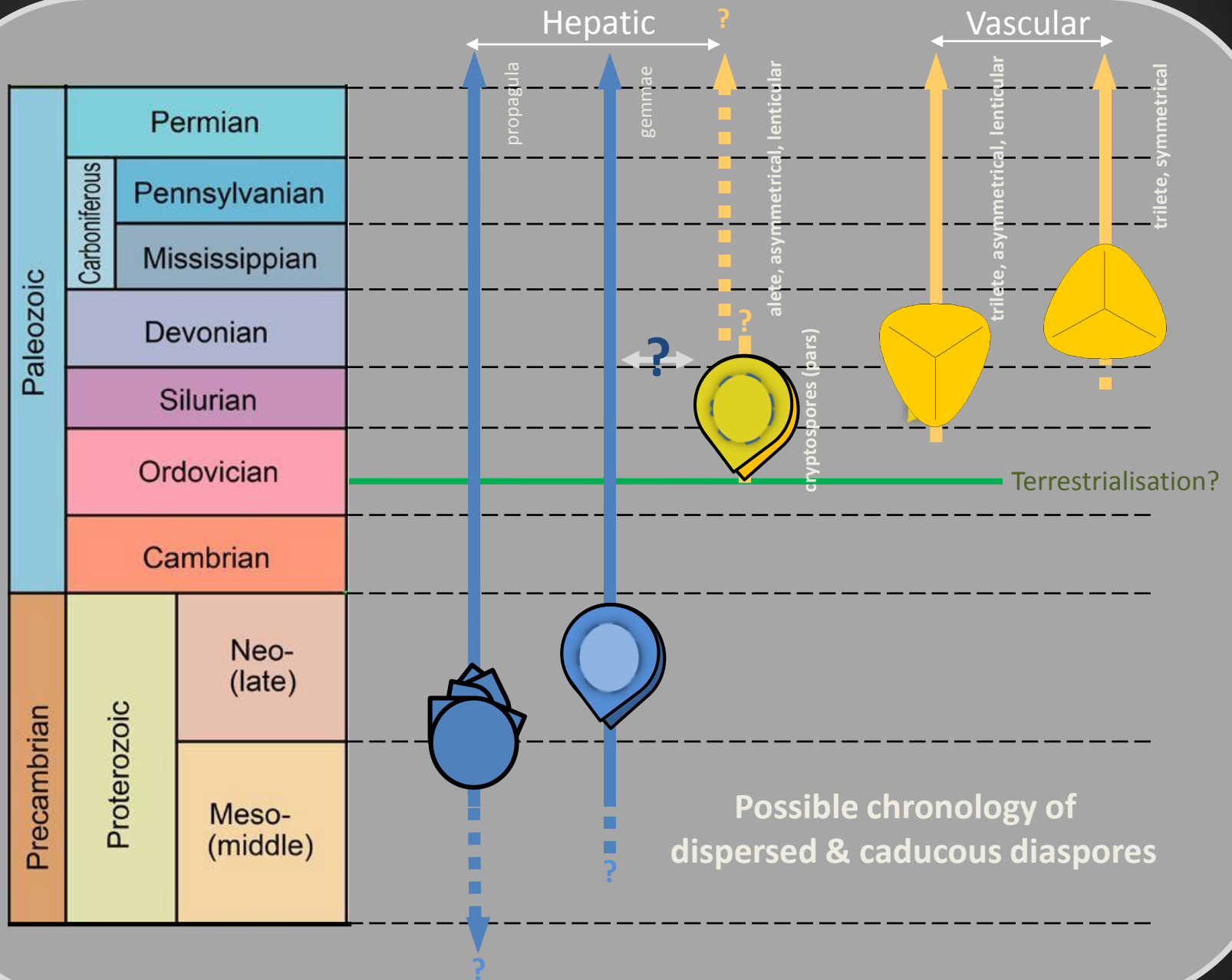
Teichertodium

distal polar view



Other dehiscence?

Attached



Conclusions

Attached reproductive cells are common in many palynological samples, but have almost exclusively been misidentified as dispersed spores.

The Microfolium is a high level taxonomic criterion of certain diaspores that has been so far completely overlooked.

Gemmae and other vegetative propagules of hepatic plants are abundant in the fossil record and nearly ubiquitous in Mid Ordovician and younger sediments.

Many have already been published as pteridophytic and lycophytic spores, cryptospores, pollen, dinocysts and acritarchs. Need to reassess their affinities.

Macrofossils of the earliest land plants are uncommon, so fossil gemmae offer a great opportunity for further advancement in the understanding of the phylogeny of early embryophytes, together with the evolutionary steps that enabled colonisation of the terrestrial environment during the Lower Palaeozoic.

Some pre-embryophytic acritarchs have gemmae-like morphology; -ancestral algae? or earlier terrestrialisation (Strother *et al.* 2011).

Emendation/replacement of the term miospore?