MICROFOSSILS IN POLAR ICE CORES

A BEGINNER'S MANUAL FOR POLLEN, SPORE, AND MICROSCOPIC CHARCOAL ANALYSIS

Authors: **Sandra O. Brugger[1,2,*], Alita Regi[3,*], Nathan J. Chellman[1], Sophia Wensman[1], Joseph R. McConnell[1]**

[1] Division of Hydrologic Sciences, Desert Research Institute, Reno NV, USA
[2] Montana State University, Bozeman MT, USA
[3] Division of Atmospheric Sciences, Desert Research Institute, Reno NV, USA
[*] Both authors contributed equally and are considered joint first authors

Table of content

A brief Introduction to ice palynology

Palynology is the "study of dust" (Greek: παλύνω = Palynō). Analyses of contemporary and fossil palynomorphs (paleopalynology) includes pollen and spores from plants, fungi, algae, etc. Palynology is used in genetic & evolutionary studies, melissopalynology (honey), allergy studies, meteorological pollen forecast, forensic field, and paleoecology (Lang 1994). Pollen are part of the reproductive cycle of plants: The male gametophyte generation housing in the pollen grain results from cell division involving a reduction by half of the chromosome content (Meiosis). Pollen needs dispersal to fulfill its biological function (i.e., fertilization of a “plant egg”). Pollen production and dispersal of plant species varies. For example, wind-pollinated plant species have a much higher production compared to insect or other animal-pollinated species because of a larger number of grains “getting lost” on their way (Lang 1994). Pollen and other palynomorphs are deposited in sediments of lakes, peatbogs, and ice sheets, where they preserve over millennia and provide information on vegetation history (e.g., Rey et al. 2019). Pollen grains have three characteristics that make them especially suitable for studying the changes in flora and vegetation:

- They are ubiquitous in the environment,
- highly resistant to decay (under anoxic conditions), and
- their morphology varies according to their botanical group, making them identifiable to the plant genus- or family-, and in some cases to the species level.

Lake sediments and peatbog pollen sequences have been analyzed for over a century (Manten 1966). Ice palynology is a much younger field (Fredskild & Wagner 1974). A few microfossil studies have been established from ice cores in the Alps (Brugger et al. 2021), Altai mountains (Nakazawa & Fujita 2006; Eichler et al. 2011; Brugger et al. 2018b), Andes (Reese & Liu 2002; Reese et al. 2003; Liu et al. 2005, 2007; Brugger et al. 2019b), Tibetan Plateau (Yang et al. 2008), and even from polar ice caps (Short & Holdsworth 1985; Koerner et al. 1988; Bourgeois 2000; Bourgeois et al. 2000; Hicks & Isaksson 2006), and recently ice caves (Feurdean et al. 2011; Leunda et al. 2019).. Earlier ice core studies mostly used pollen dating purposes (seasonality of pollen production) or pollen as an indicator for wind directions and source area estimates (Fredskild & Wagner, 1974; Bourgeois, 2000; Nakazawa et al., 2004, 2005). These earlier studies did not fully exploit the paleoecological potential of pollen from ice archives. Recent methodological advances permit the study of microfossils even from remote ice cores in Central Greenland (Brugger et al., 2019a, in press). Microfossil records from these remote ice cores have many advantages compared to traditional sediment-based records including:

- Ice cores often provide well-preserved pollen grains,
- allow for contiguous records,
- contain relatively low concentrations of dust and other non-pollen debris,
- have a large footprint of ecosystem change reflected in a single record,
- chronological precision of +/- a few years,
- contain many other climate / environmental proxies for direct comparison,
- allow for high temporal resolution for comparison with historical sources, tree-ring data etc.

Ice core disadvantages for palynology compared to lake/peat sediment cores:

- Ice microfossil records are prone to lab contamination due to low microfossil concentrations,
- Have a risk for microfossil damage and loss during chemical treatment with acids,
- Contain low microfossil concentrations (<100 grains L^{-1} vs. >100,000 grains cm^{-3} in sediments),
- Require time consuming analyses due to unfavorable microfossil to marker spore ratios,
- Often have more complex source areas than local lake sediments with diverse floristic composition from many ecosystems combined in a single record (Brugger et al. 2018a).

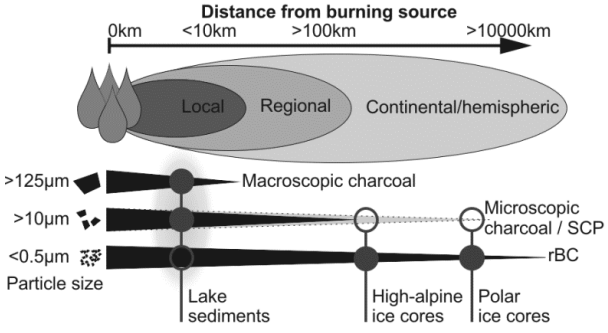
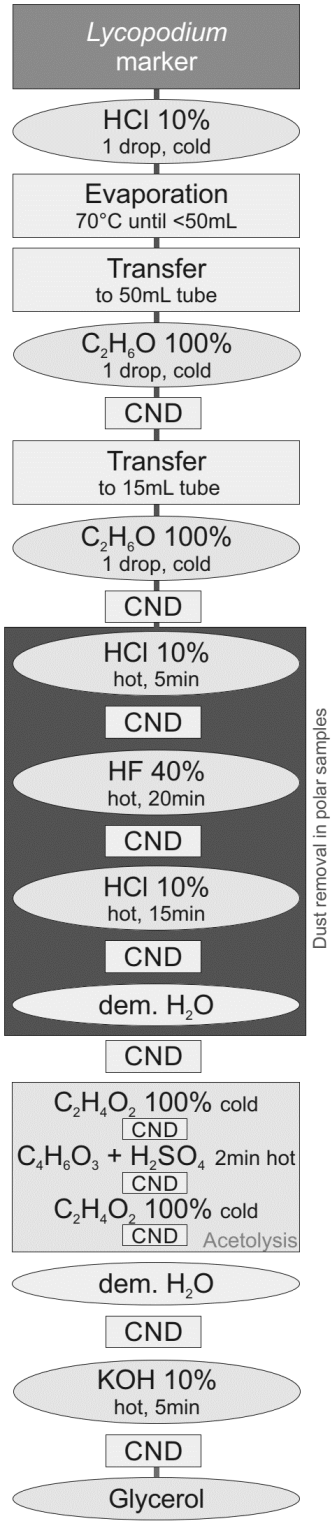
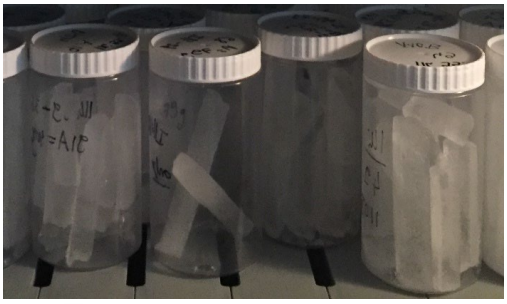


Figure 1 Source areas of microfossils in different natural archives.

Microfossil extraction protocol for polar ice samples

Laboratory steps for pollen extraction





Aim of the protocol for microfossil extraction from ice samples: A concentrated microfossil sample on a microscopic slide:

- Removal of cell content for facilitated pollen identification
- Removal of potentially obscuring particles/impurities
- Counting of an adequate number of pollen grains, spores, and other microfossils to reconstruct past ecosystem change

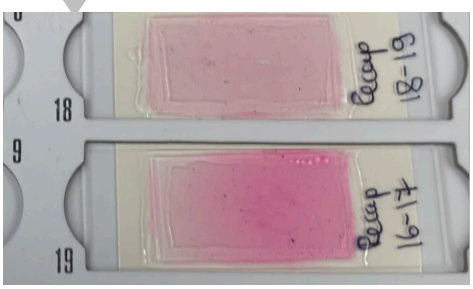


Figure 2 Laboratory protocol adapted for pollen extraction from polar ice samples with indication of additional dust removal procedure (red shading). See Brugger et al. (2018a) for details on original method.

Introducing terminology for pollen determination

In fossil pollen assemblages, only the very durable skeleton (pollen wall) made of sporopollenin, is preserved. The pollen wall consists of several layers:

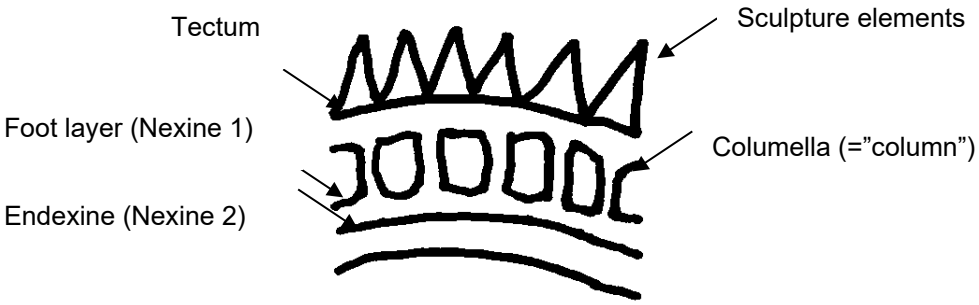
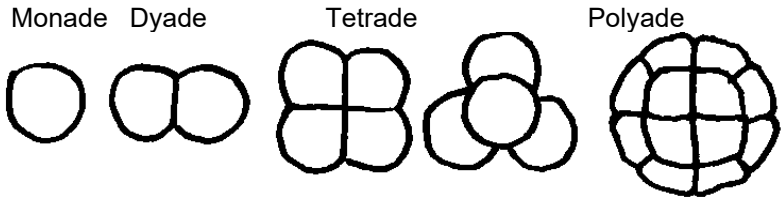


Figure 3 The components of a pollen wall (adapted from Lang 1994).

The nexine consists of an endexine (Nexine 2 and a footlayer (nexine 1). The sexine consists of columella (sexine 1), the tectum (sexine 2) and sculptural elements (sexine 3). The footlayer together with the sexine is also called Ektexine, separating these wall components from the endexine (Lang 1994).

These fossil pollen skeletons can be determined by a number of characteristics such as the pollen grain shape, size, apertures, wall ornamentations, etc.:

- **Pollen unit**



- **Grain size** (Beug 2004)

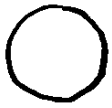
Taxon	**Size**
Urtica (Family of nettles)	~3-5 µm
Corylus/*Betula* (Hazel, Birch)	~25-30 µm
Tilia (Linden/basswood)	~50 µm
Pinus (Pine)	~90-100 µm
Picea (Spruce)	~200 µm
Abies (Fir)	~280 µm

- **Vesiculate vs. non-vesiculate**

  - One or several sacchi (airbladders)

- **Shape**
  - Spheroidal = grain is as long as wide (length to width ratio is 0.75 to 1.33)
  - Oblate = grain has a much larger equatorial length compared to pole length (length to width ratio is <0.75) → appears flat
  - Prolate grain has a much smaller equatorial length compared to pole length (length to width ratio is >1.33) → appears long

- **Apertures**
  - Inaperturate

    
  - Porate (porus, pl. pori) = round openings

    Monoporate Diporate Triporate Stephanoporate Peri-/pantoporate

    
  - Poroide = indistinct openings (i.e., thinning of walls in Cyperaceae)
  - Colpate (colpus, pl. colpi) = elongated openings

    Monocolpate Dicolpate Tricolpate Stephanocolpate Pericolpate

    Syncolpate

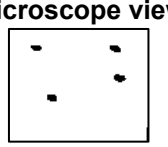
    
  - Colporate = opening is a combination of pori and colpi

    Tricolporate Stephanocolporate Heterocolpate

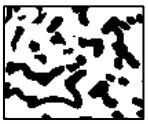
    
  - Fenestrate (Window-like apertures)

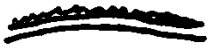
- **Ornamentation** **Microscope view** **Tectate** **Semi-/Intectate**
  - Psilate
    “Smooth surface”

    
  - Scabrate/Granulate
    “Sandpaper surface”

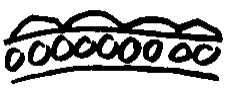
    
  - Rugulate
    “Sausages on the surface”

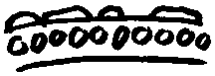
    
  - Verrucate
    “Warts-like surface”

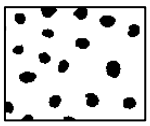
- Reticulate
  "Net-like"


- Striate
  "Net with direction"



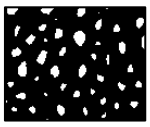
- Perforate
  "Little holes"




- Gemmate
  "Single warts"


- Echinate
  "Conical spikes"


- Baculate
  "Columella without tectum"




- **Some other features**
  - Margo = wall thinning towards apertures

  - Costae = endexine wall thickening towards apertures

  - Vestibulum = inner and outer wall separate towards aperture

  - Operculum = "lid on top of pore"

  - Anulus = thickened ring around pore

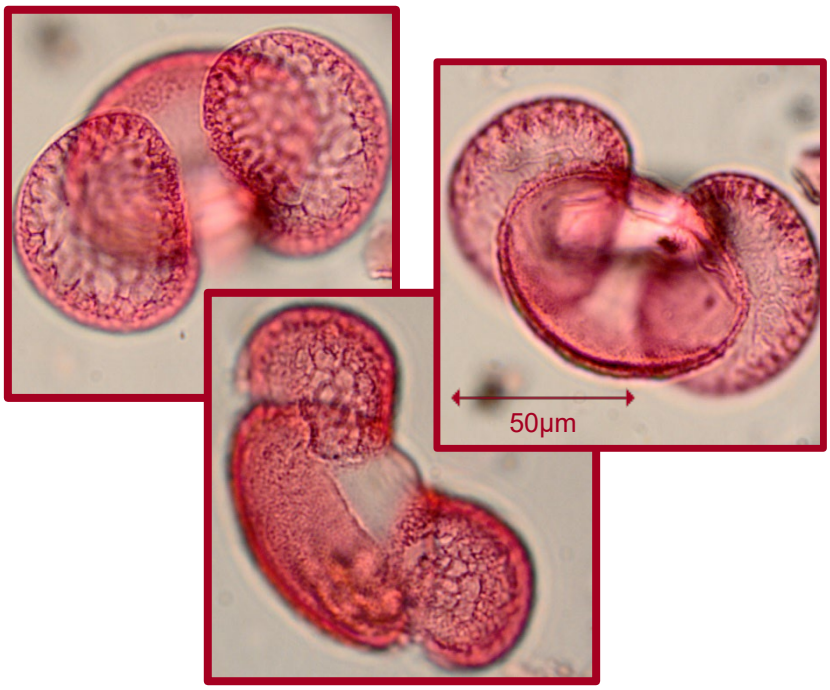
Common microfossils in Greenland ice

All pollen and spore pictures shown in this manual originate from the RECAP (REnland ice CAP project) ice core in East Greenland (71.30°N, 26.72°W, 2315 m a.s.l.) spanning ca 6000 years BCE to 1850 CE. Pollen determination followed Moore et al. (1991), Beug (2004), Clegg et al. (2005), and PalDat (2000).

Vesiculate pollen

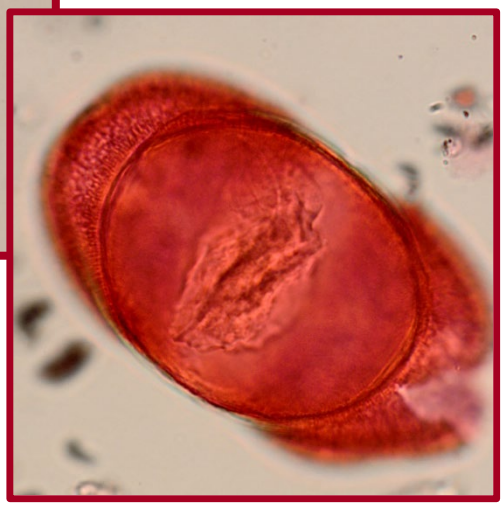
Pinus

Size: 70-100 µm
Shape: vesiculate
Dispersal unit: monad
Openings: inaperturate
Other notes: sacchi more than half round and clearly separated from pollen body, even pollen wall



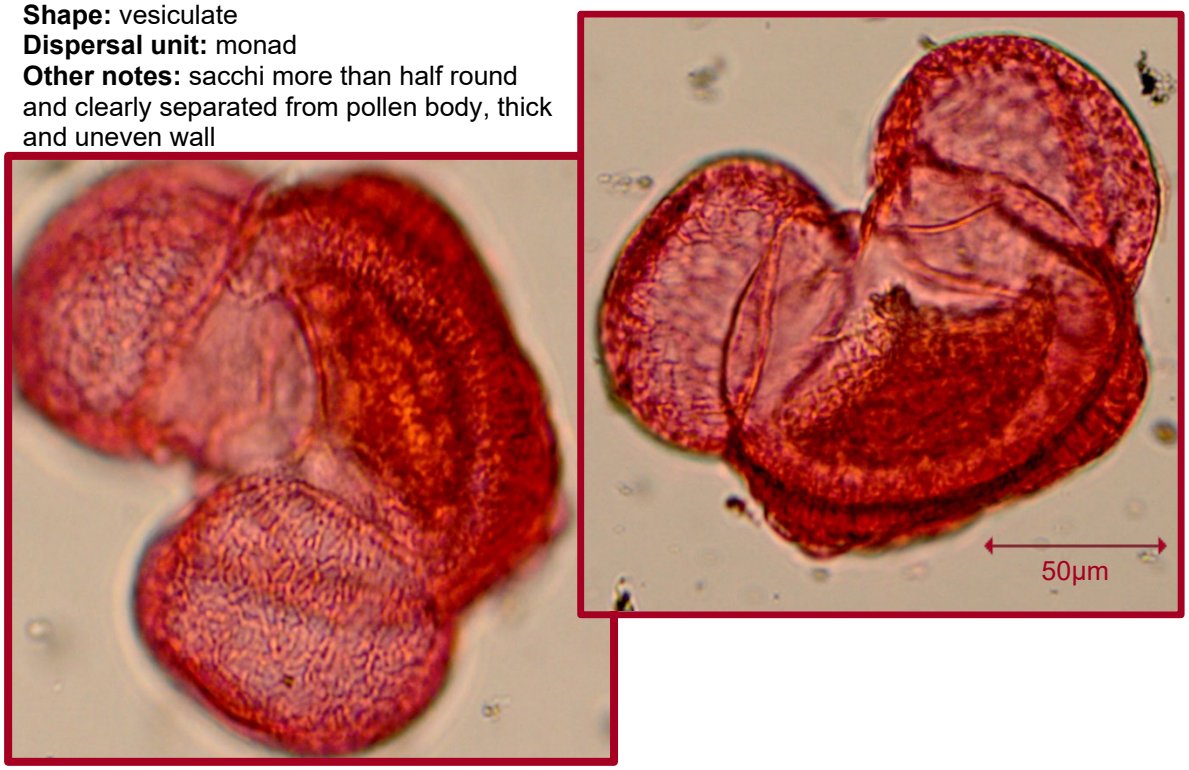
Picea

Size: 100-150 µm
Shape: vesiculate
Dispersal unit: monad
Other notes: sacchi half round and not clearly separated from pollen body



Abies

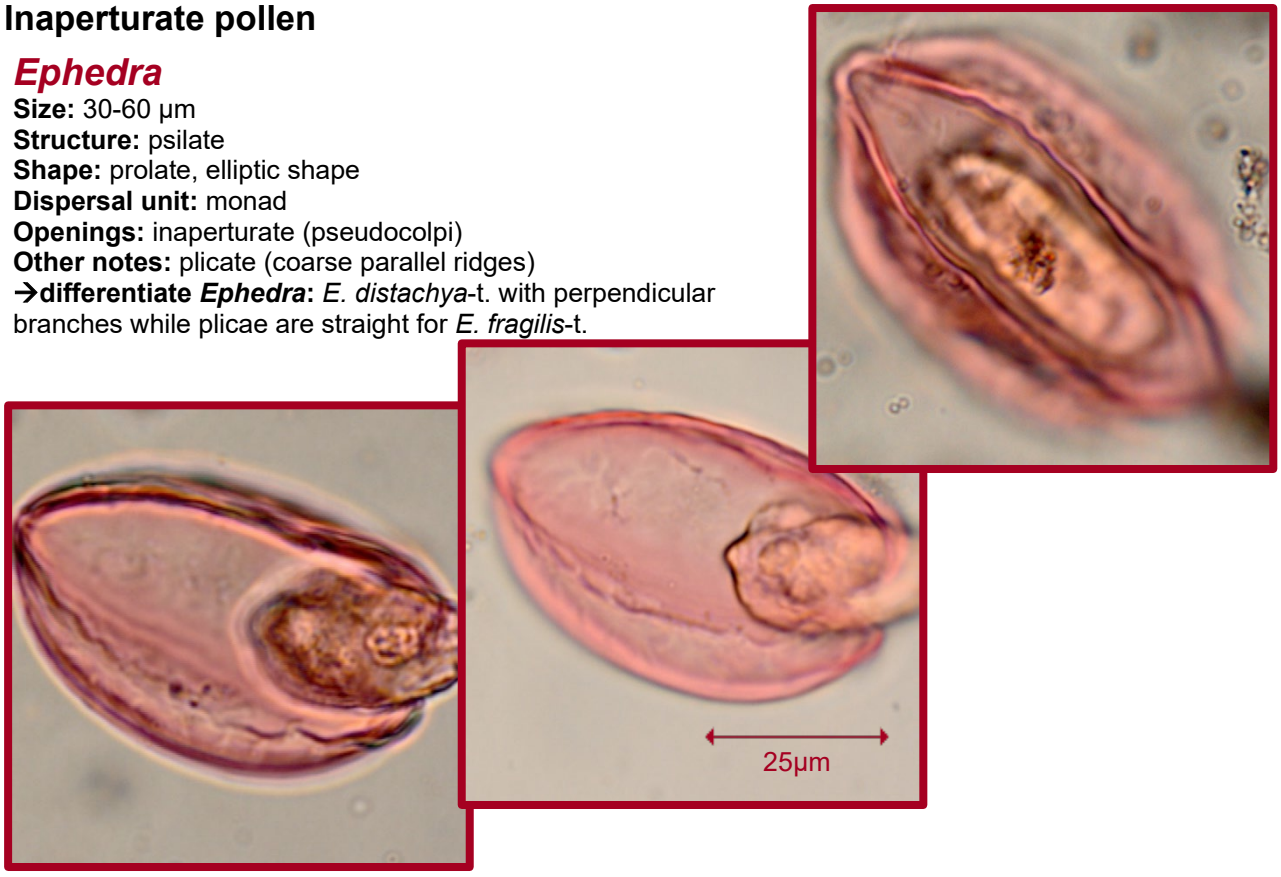
Size: 100-200 µm
Shape: vesiculate
Dispersal unit: monad
Other notes: sacchi more than half round and clearly separated from pollen body, thick and uneven wall



Inaperturate pollen

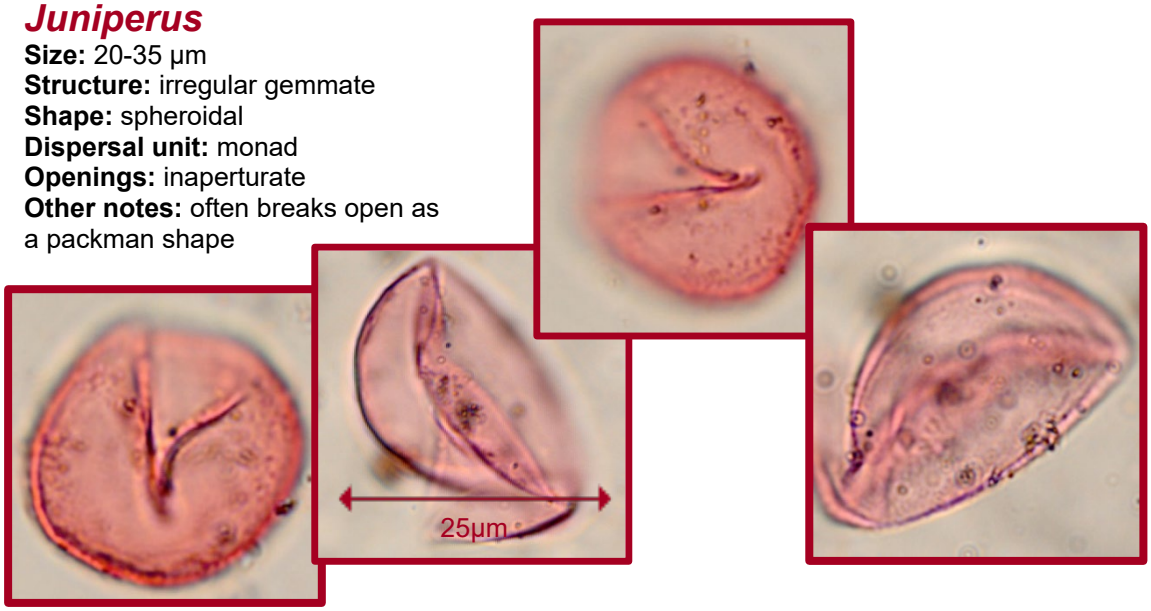
Ephedra

Size: 30-60 µm
Structure: psilate
Shape: prolate, elliptic shape
Dispersal unit: monad
Openings: inaperturate (pseudocolpi)
Other notes: plicate (coarse parallel ridges)
→**differentiate *Ephedra*:** *E. distachya*-t. with perpendicular branches while plicae are straight for *E. fragilis*-t.



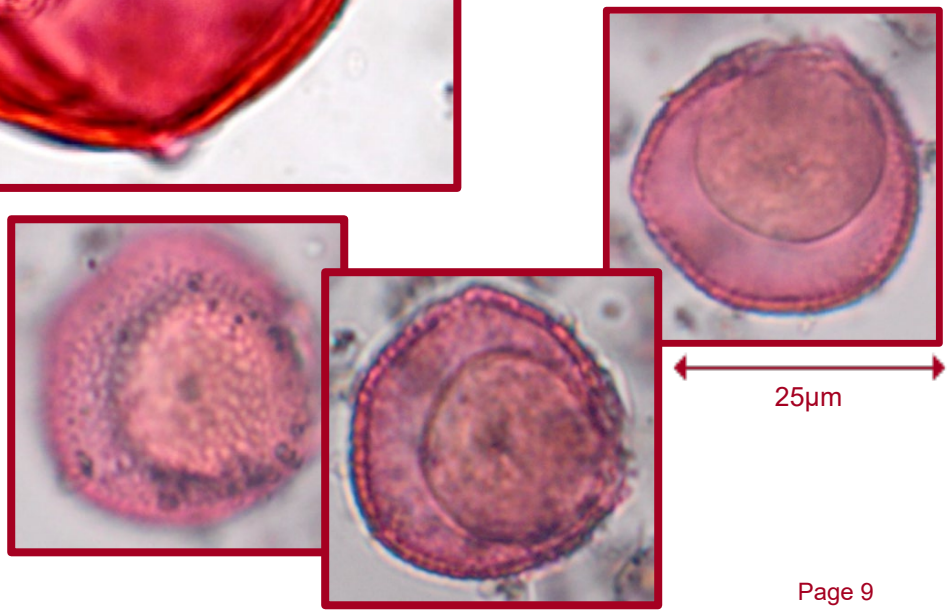
Juniperus

Size: 20-35 µm
Structure: irregular gemmate
Shape: spheroidal
Dispersal unit: monad
Openings: inaperturate
Other notes: often breaks open as a packman shape



Larix

Size: 60-100μm
Structure: psilate
Shape: spheroidal, often uneven shape
Dispersal unit: monad
Openings: inaperturate
Other notes: pollen wall often with irregular folding



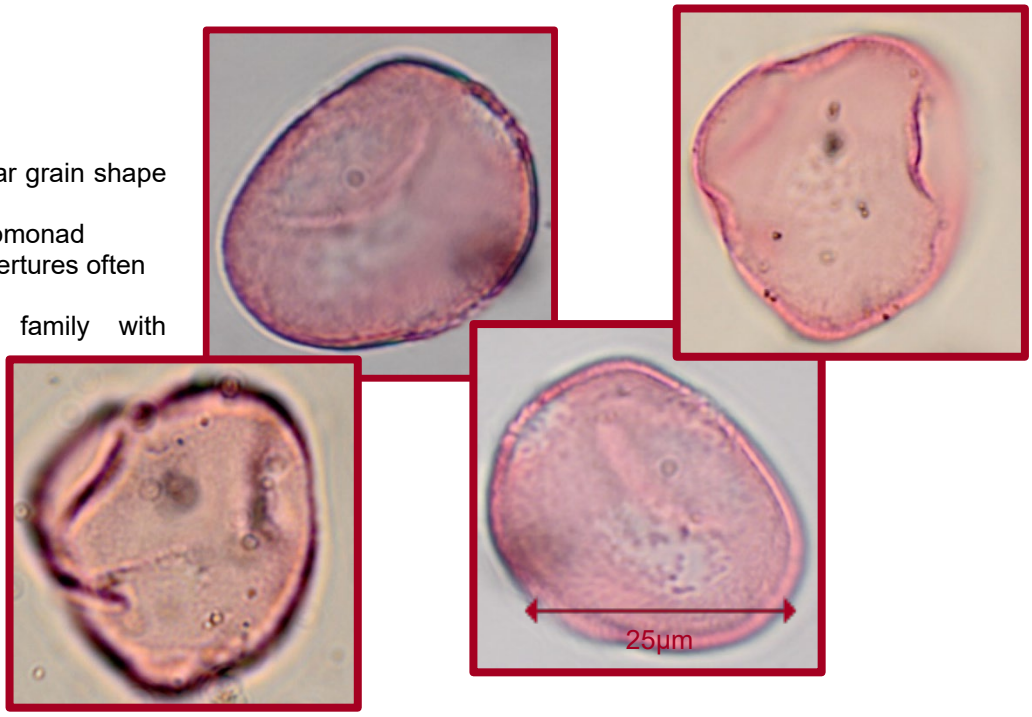
Populus

Size: 20-35µm
Structure: reticulate
Shape: spheroidal
Dispersal unit: monad
Openings: inaperturate

Poroid pollen

Cyperaceae

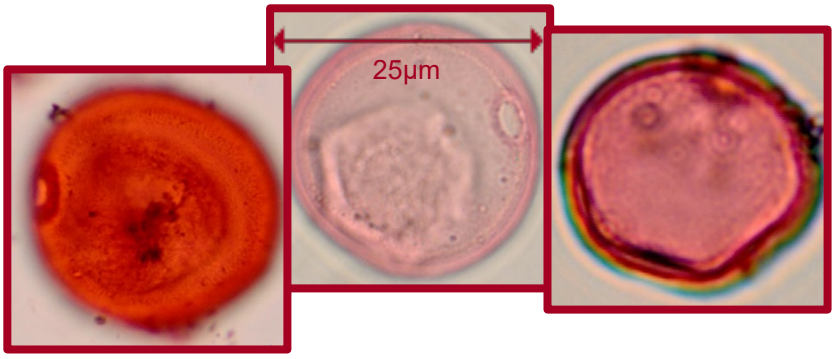
Size: 25-50 µm
Structure: scabrate
Shape: prolate, irregular grain shape like potato bag
Dispersal unit: pseudomonad
Openings: poroide, apertures often elongated
Other notes: large family with variable pollen types

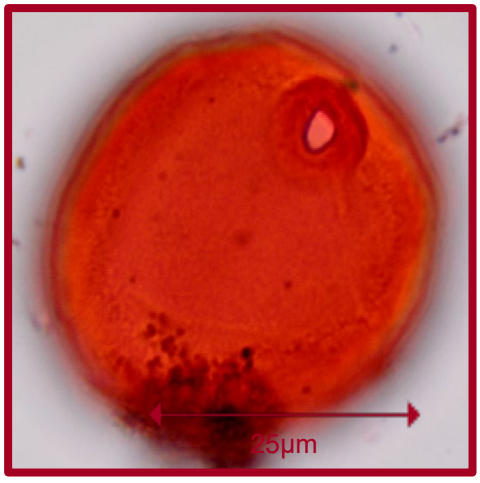


Porate pollen

Poaceae

Size: 20-100 µm
Structure: psilate-scabrate
Shape: spheroidal to prolate
Dispersal unit: monad
Openings: monoporate, anulus, operculum



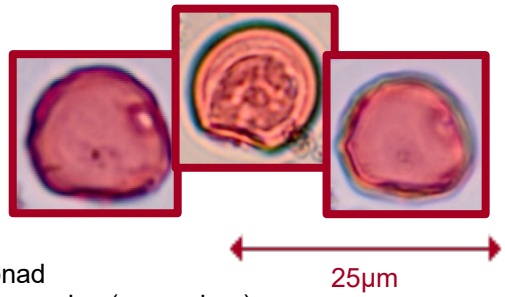


Cerealia-t.

Size: >37 µm
Structure: psilate-scabrate
Shape: spheroidal to prolate
Dispersal unit: monad
Openings: monoporate, anulus, operculum
→differentiate Cerealia-t.: Cerealia-t. is larger in grain size, anulus thickness, width and diameter compared to other Poaceae following Beug (2004)

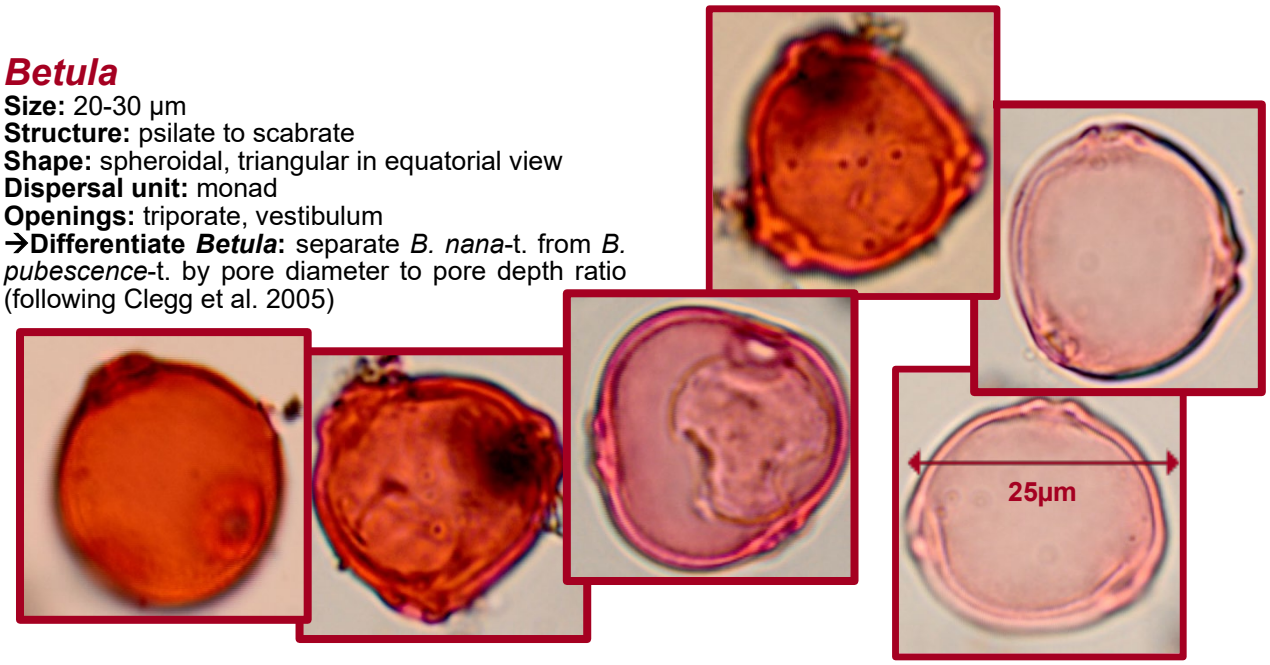
Urtica

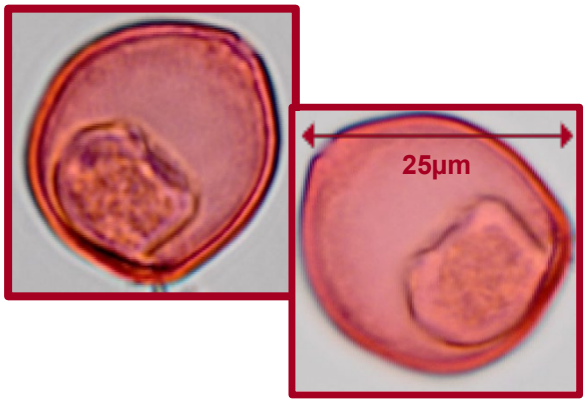
Size: 10-20 µm
Structure: psilate
Shape: spheroidal
Dispersal unit: monad
Openings: triporate, anulus (operculum)



Betula

Size: 20-30 µm
Structure: psilate to scabrate
Shape: spheroidal, triangular in equatorial view
Dispersal unit: monad
Openings: triporate, vestibulum
→**Differentiate *Betula*:** separate *B. nana*-t. from *B. pubescence*-t. by pore diameter to pore depth ratio (following Clegg et al. 2005)



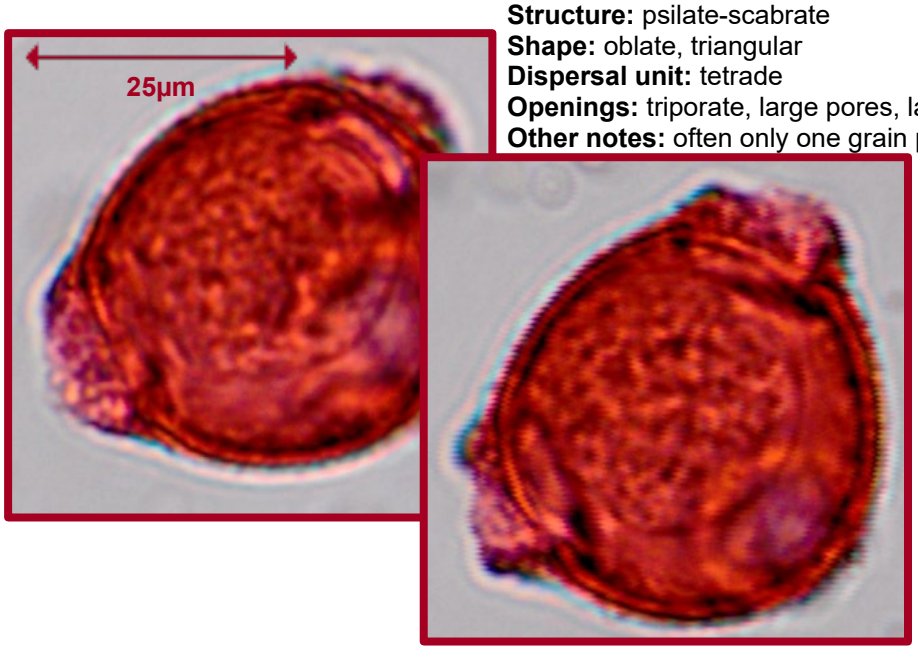


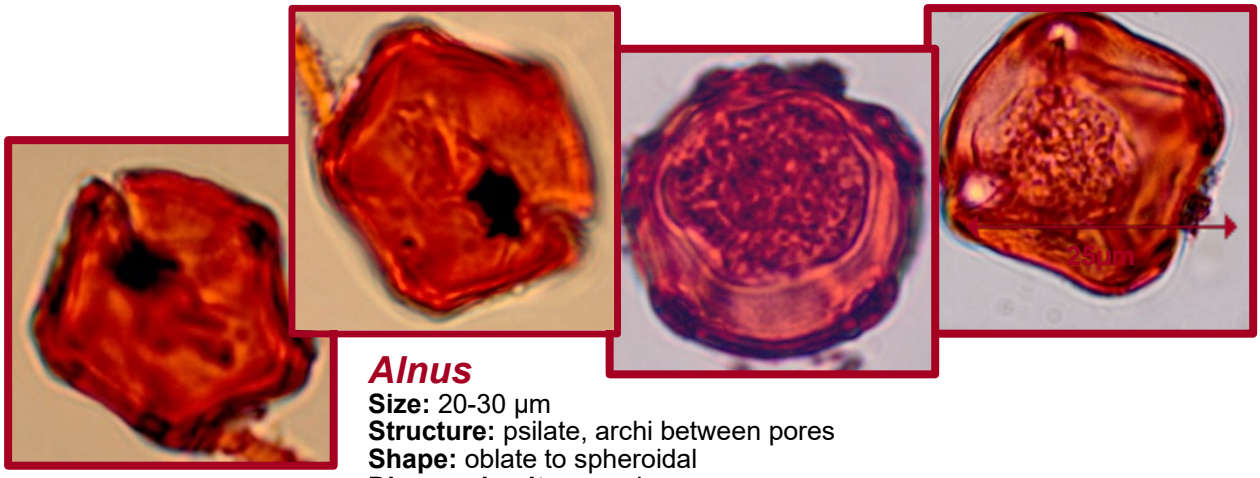
Corylus

Size: 25-30 µm
Structure: psilate to scabrate
Shape: spheroidal, triangular in equatorial view
Dispersal unit: monad
Openings: triporate, no vestibulum

Epilobium

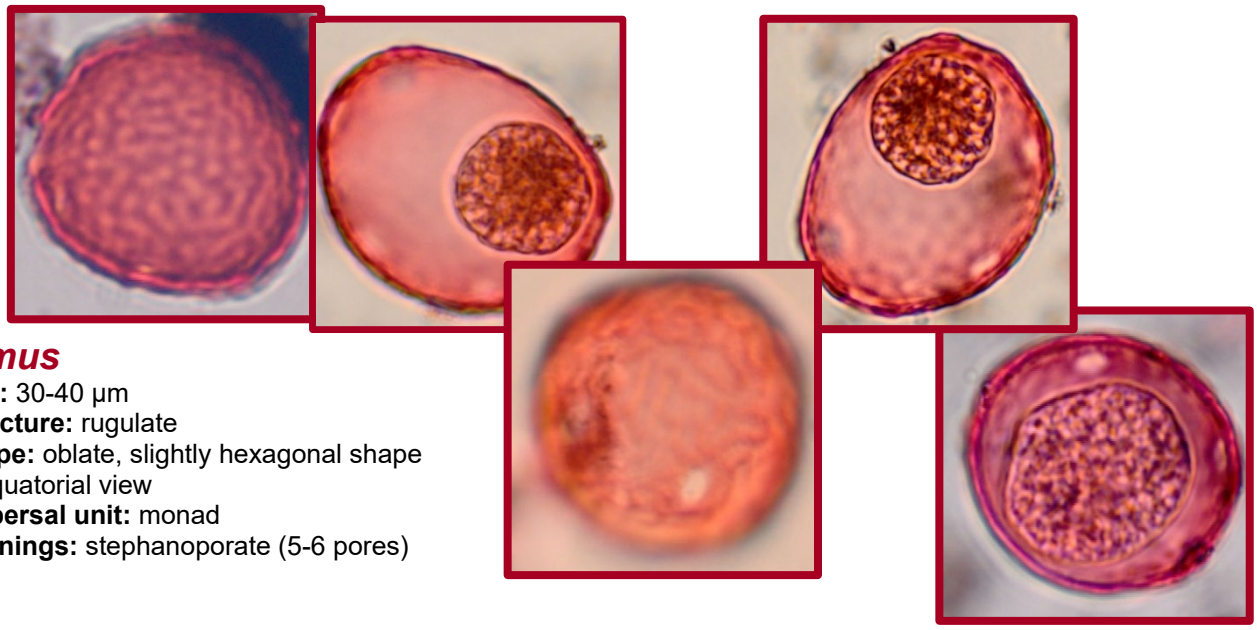
Size: 50-100 µm
Structure: psilate-scabrate
Shape: oblate, triangular
Dispersal unit: tetrade
Openings: triporate, large pores, large conical vestibulum
Other notes: often only one grain preserved





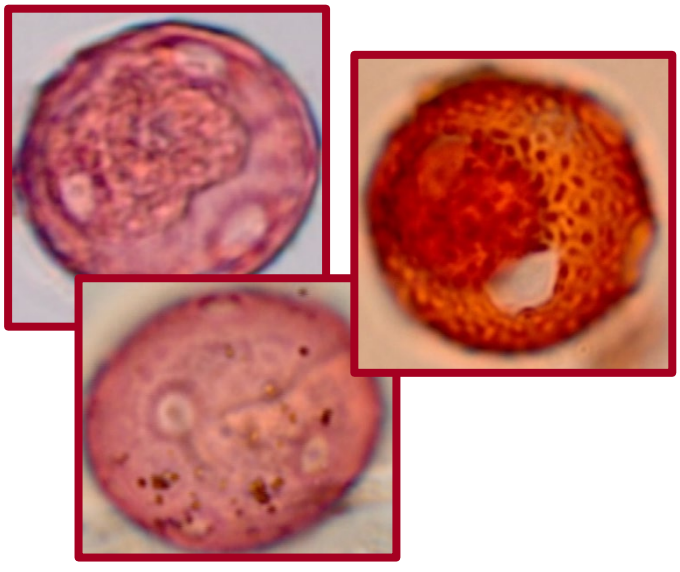
Alnus

Size: 20-30 µm
Structure: psilate, archi between pores
Shape: oblate to spheroidal
Dispersal unit: monad
Openings: stephanoporate (4-6 pores), vestibulum
Differentiate *Alnus*: *A. glutinosa*-t. with broad and clearly defined archi and *A. viridis* archi like sharp folds



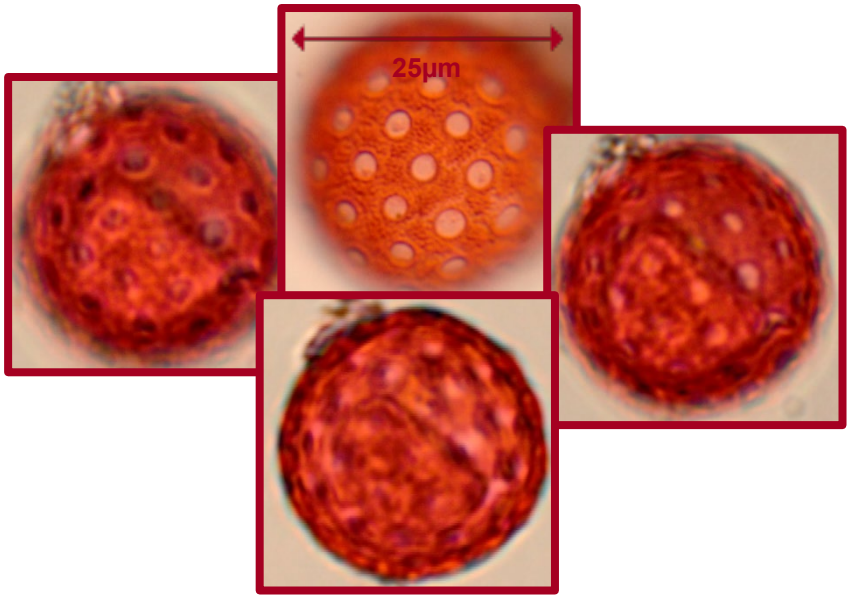
Ulmus

Size: 30-40 µm
Structure: rugulate
Shape: oblate, slightly hexagonal shape in equatorial view
Dispersal unit: monad
Openings: stephanoporate (5-6 pores)



Plantaginaceae

Size: 20-35 µm
Structure: scabrate-verrucate
Shape: spheroidal
Dispersal unit: monad
Openings: poliporate (6-20 pores) with or without anulus, with or without operculum, pores often not clearly separated if without anulus
→**Differentiate *Plantaginaceae:*** *P. lanceolata* with clear anulus and presence of operculum, see Beug (2004) for differentiation of further Plantaginaceae types

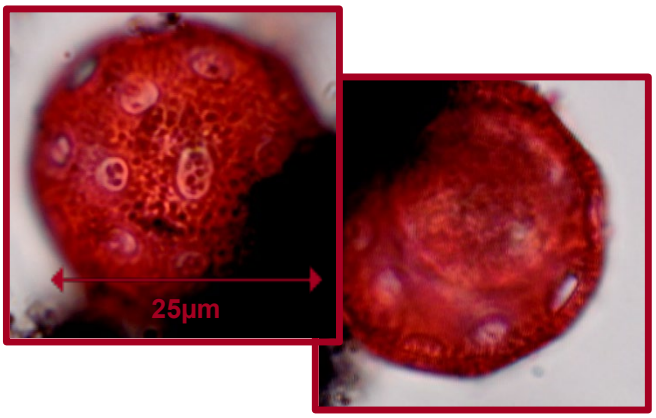


Amaranthaceae

Size: 18-40 µm
Structure: psilate
Shape: spheroidal
Dispersal unit: monad
Openings: periporate (25-50 pores)
Other notes: large family with variable pollen types

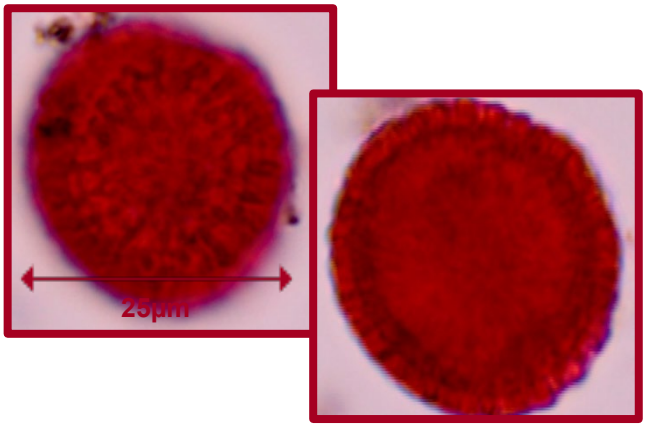
Caryophyllaceae

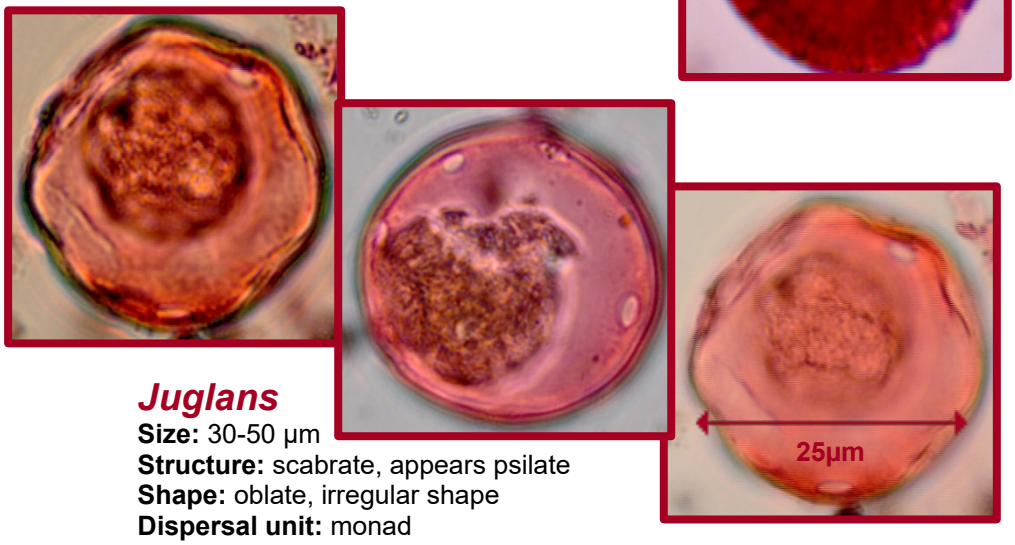
Size: 25-50 µm
Structure: scabrate-perforate
Shape: spheroidal
Dispersal unit: monad
Openings: periporate (10-40 pores), operculate, often with anulus
Other notes: aperture membrane ornamented



Daphne

Size: 20-40 µm
Structure: reticulate, high muri and short columella
Shape: spheroidal
Dispersal unit: monad
Openings: periporate, pores not clearly defined

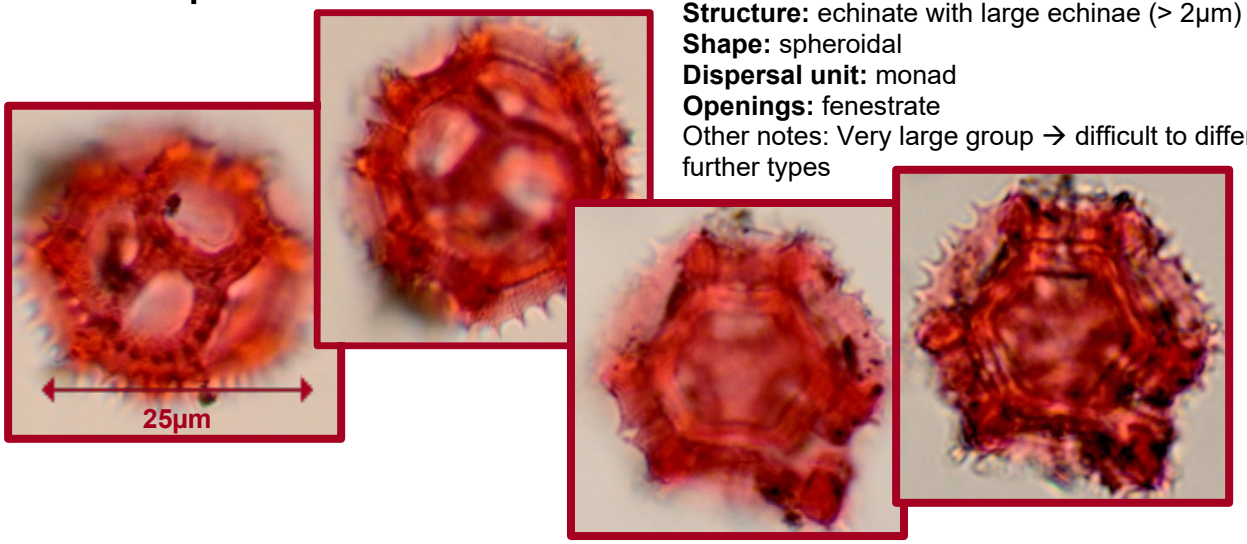




Juglans

Size: 30-50 µm
Structure: scabrate, appears psilate
Shape: oblate, irregular shape
Dispersal unit: monad
Openings: periporate, large pori unevenly distributed, anulus

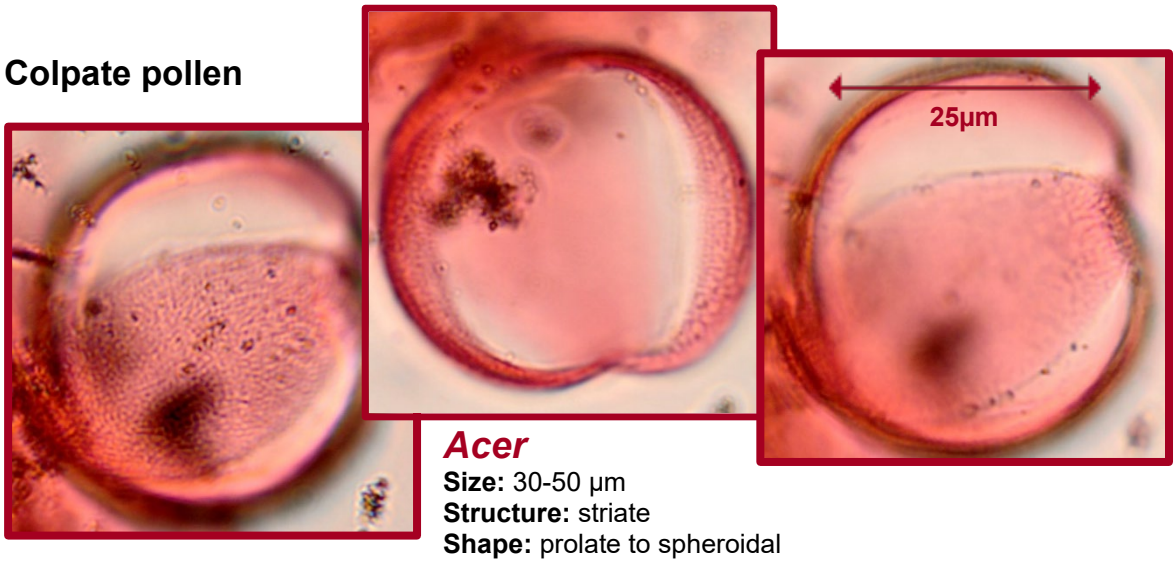
Fenestrate pollen



Cichorioideae

Size: 25-40 µm
Structure: echinate with large echinae (> 2µm)
Shape: spheroidal
Dispersal unit: monad
Openings: fenestrate
Other notes: Very large group → difficult to differentiate further types

Colpate pollen

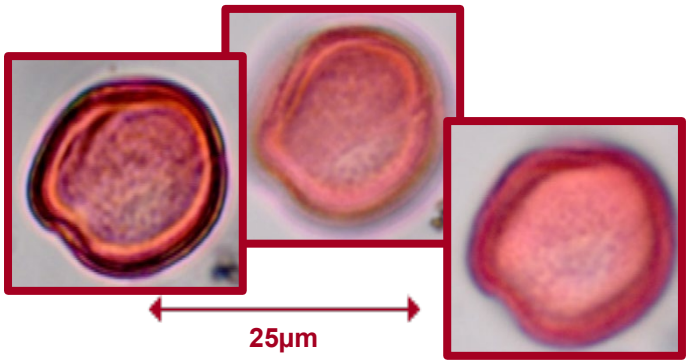


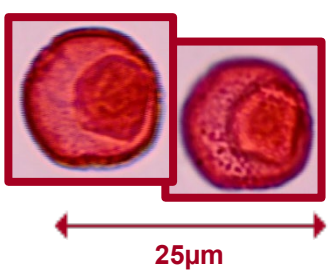
Acer

Size: 30-50 µm
Structure: striate
Shape: prolate to spheroidal
Dispersal unit: monad
Openings: tricolpate, long colpi

Papaver

Size: 20-35 µm
Structure: scabrate
Shape: spheroidal-prolate
Dispersal unit: monad
Openings: tricolpate, colpi with ornamentation



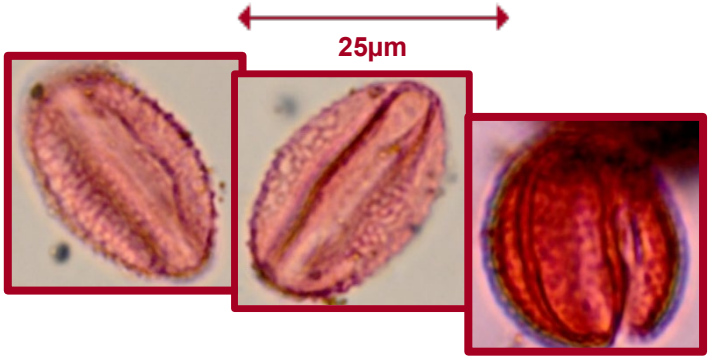


Platanus

Size: 15-25 µm
Structure: reticulate
Shape: spheroidal
Dispersal unit: monad
Openings: tricolpate, wide colpi with ornamentation

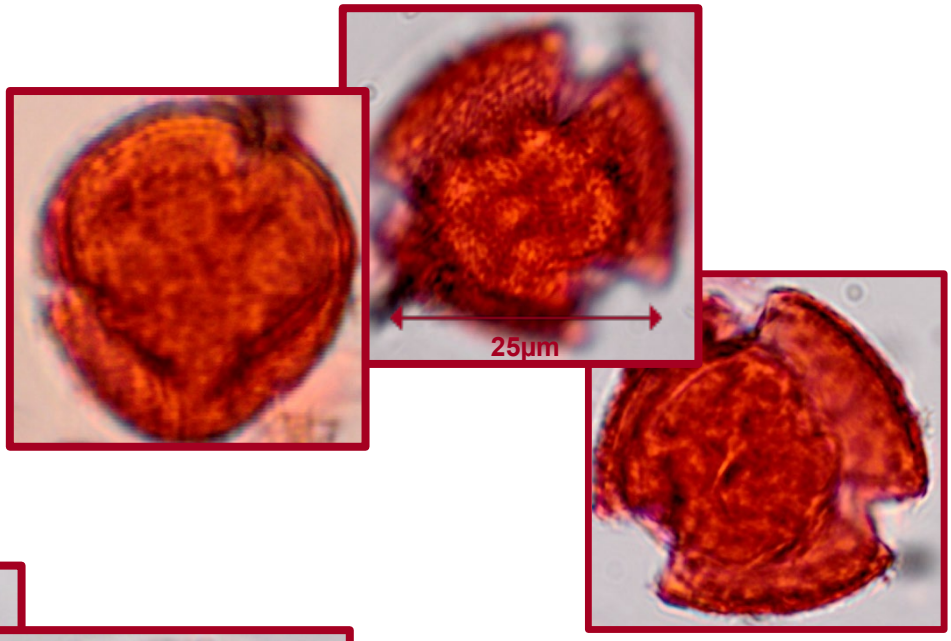
Salix

Size: 15-30 µm
Structure: reticulate with margo
Shape: prolate
Dispersal unit: monad
Openings: tricolpate (can appear tricolporoide)



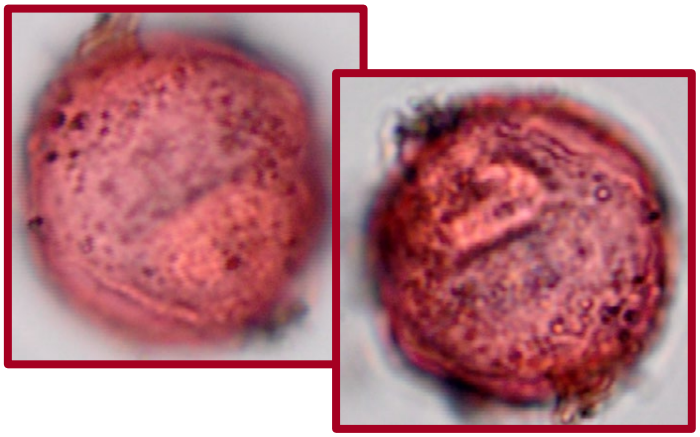
Quercus robur-t.

Size: 30-40 µm
Structure: scabrate
Shape: prolate to spheroidal
Dispersal unit: monad
Openings: tricolpate, long colpi



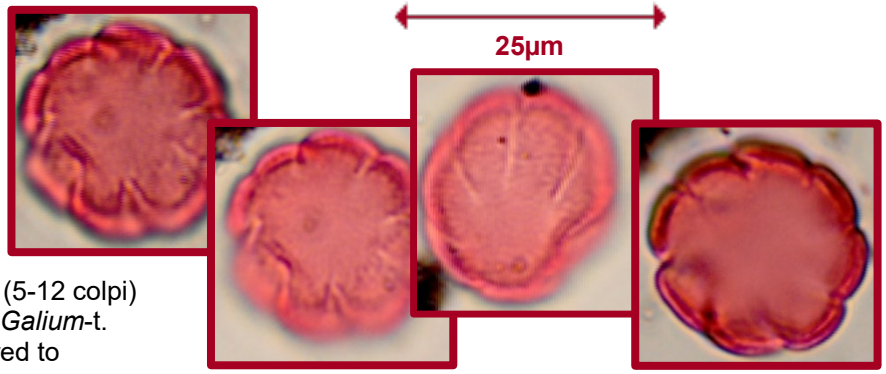
Ranunculaceae

Size: 25-50 µm
Structure: scabrate
Shape: spheroidal
Dispersal unit: monad
Openings: tri-/pericolpate, colpi with granulae



Rubiaceae

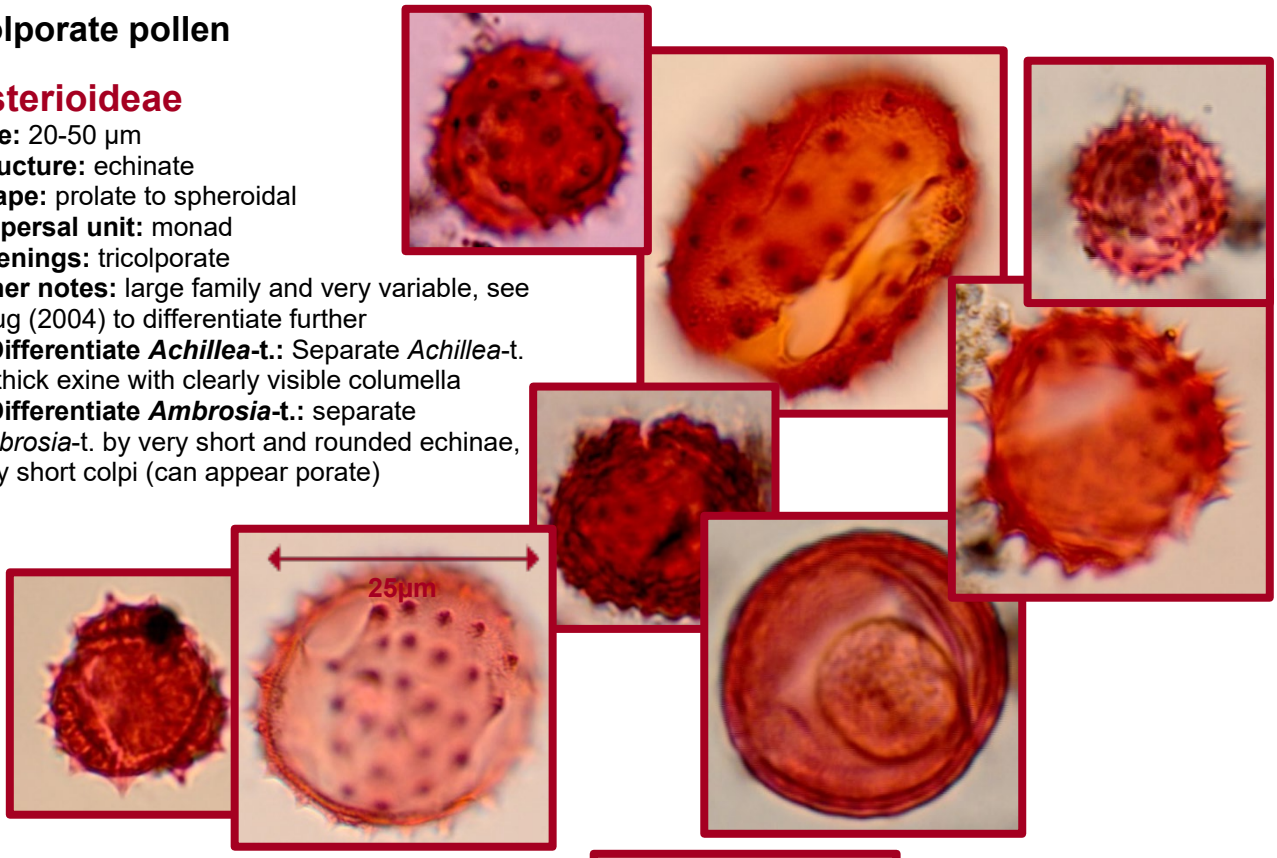
Size: 15-30 µm
Structure: psilate-reticulate
Shape: spheroidal to prolate
Dispersal unit: monad
Openings: stephanocolpate (5-12 colpi)
→Differentiate Rubiaceae: *Galium*-t. with psilate structure compared to reticulate *Mentha*-t.

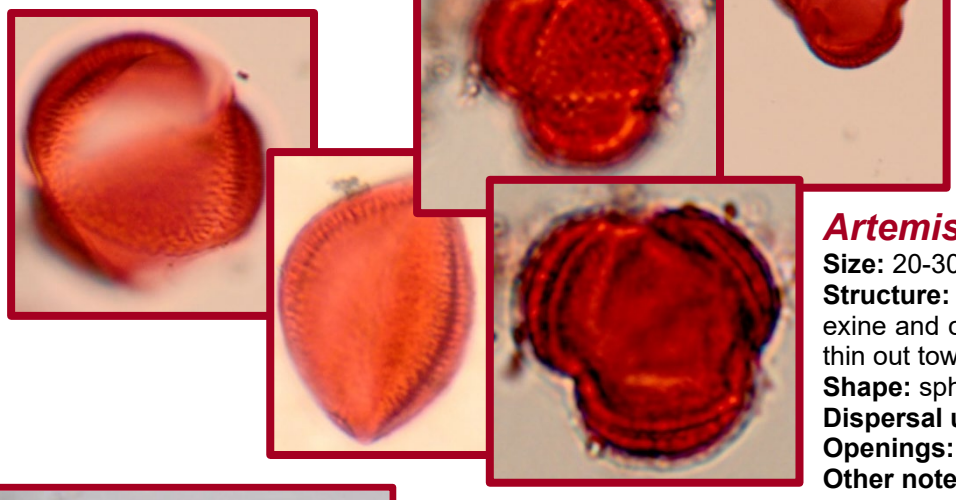


Colporate pollen

Asterioideae

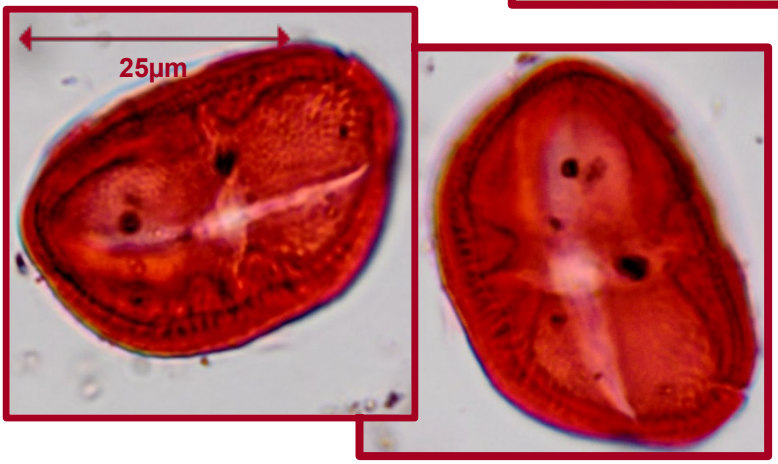
Size: 20-50 µm
Structure: echinate
Shape: prolate to spheroidal
Dispersal unit: monad
Openings: tricolporate
Other notes: large family and very variable, see Beug (2004) to differentiate further
→**Differentiate *Achillea*-t.:** Separate *Achillea*-t. by thick exine with clearly visible columella
→**Differentiate *Ambrosia*-t.:** separate *Ambrosia*-t. by very short and rounded echinae, very short colpi (can appear porate)





Artemisia

Size: 20-30 µm
Structure: microechinate, with thick exine and clearly visible columella that thin out towards openings and poles
Shape: spheroidal to prolate
Dispersal unit: monad
Openings: tricolporate
Other notes: echinae mostly invisible

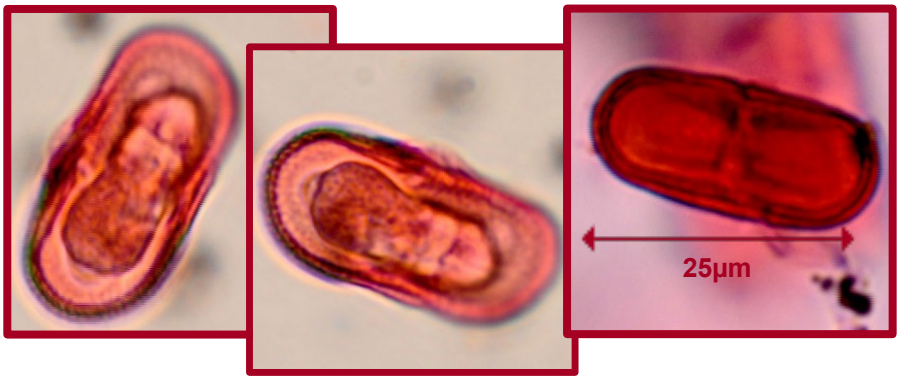


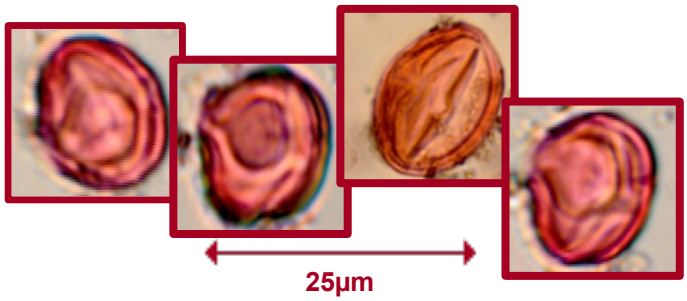
Centaurea

Size: 25-50 µm
Structure: (micro)-echinate, clearly visible collumelle and thick exine
Shape: prolate
Dispersal unit: monad
Openings: tricolporate with pronounced costae
Other notes: See Beug (2004) to differentiate *Centaurea* types

Apiaceae

Size: 20-80 µm
Structure: scabrate, appears psilate, often columelle visible, tectate
Shape: prolate, long shape
Dispersal unit: monad
Openings: tricolporate
Other notes: large family, see Beug (2004) to further differentiate Apiaceae types



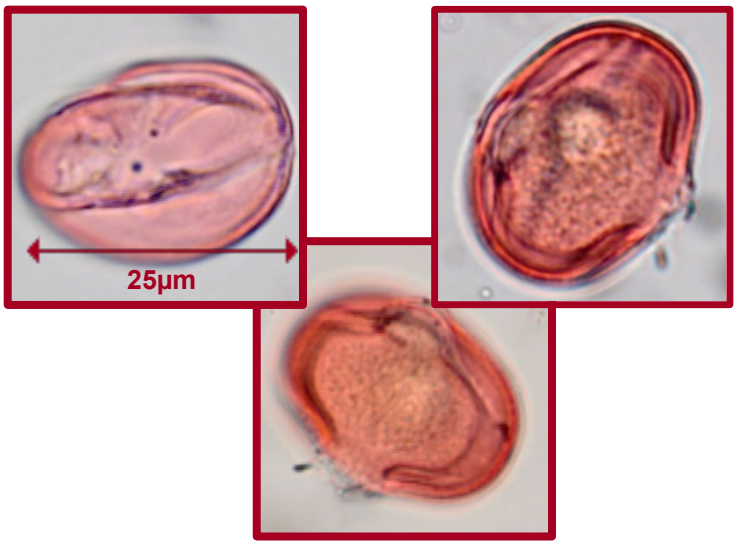


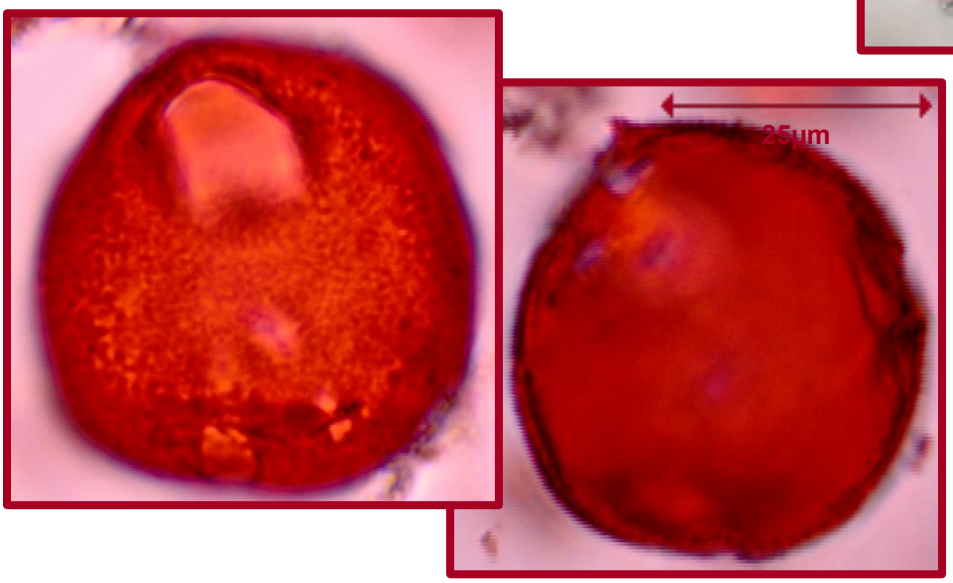
Castanea

Size: 10-20 µm
Structure: psilate
Shape: prolate
Dispersal unit: monad
Openings: tricolporate

Fabaceae

Size: 15-60 µm
Structure: psilate-reticulate
Shape: prolate, often barrel-like shape
Dispersal unit: monad
Openings: tricolporate, often large round to oval shaped pores
Other notes: large family with variable pollen types
→**Differentiate Fabaceae:** Fabaceae can be further separated with Beug (2004). Moor et al. (1991) or similar literature



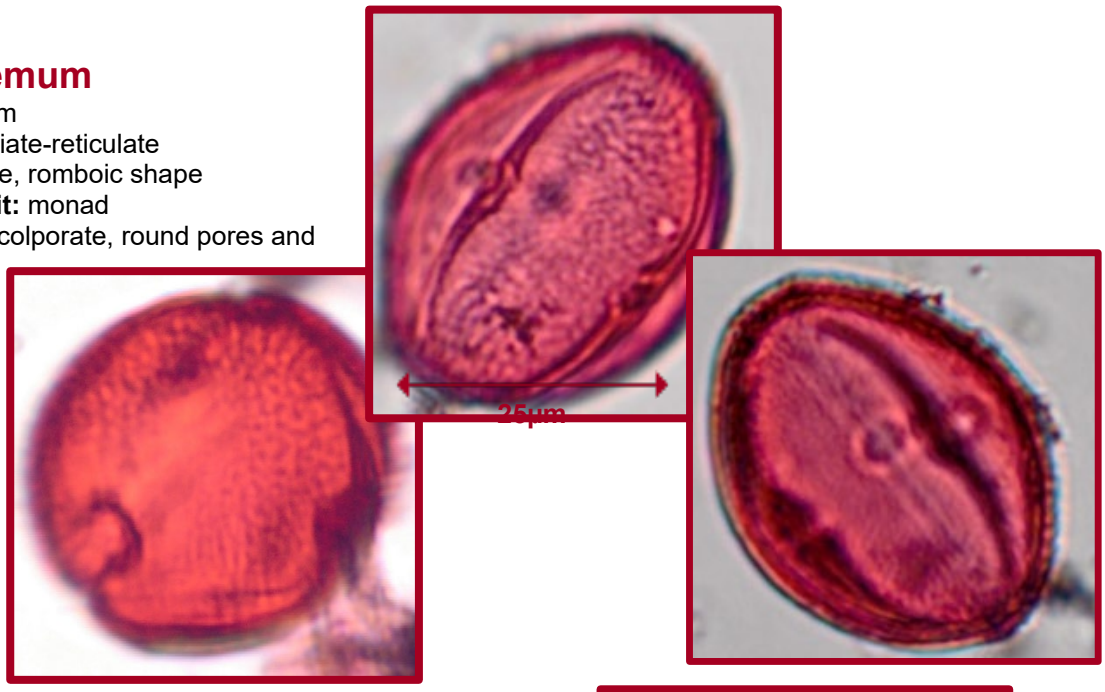


Fagus

Size: 40-50 µm
Structure: scabrate
Shape: spheroidal
Dispersal unit: monad
Openings: tricolporate, large round pores and relatively short colpi

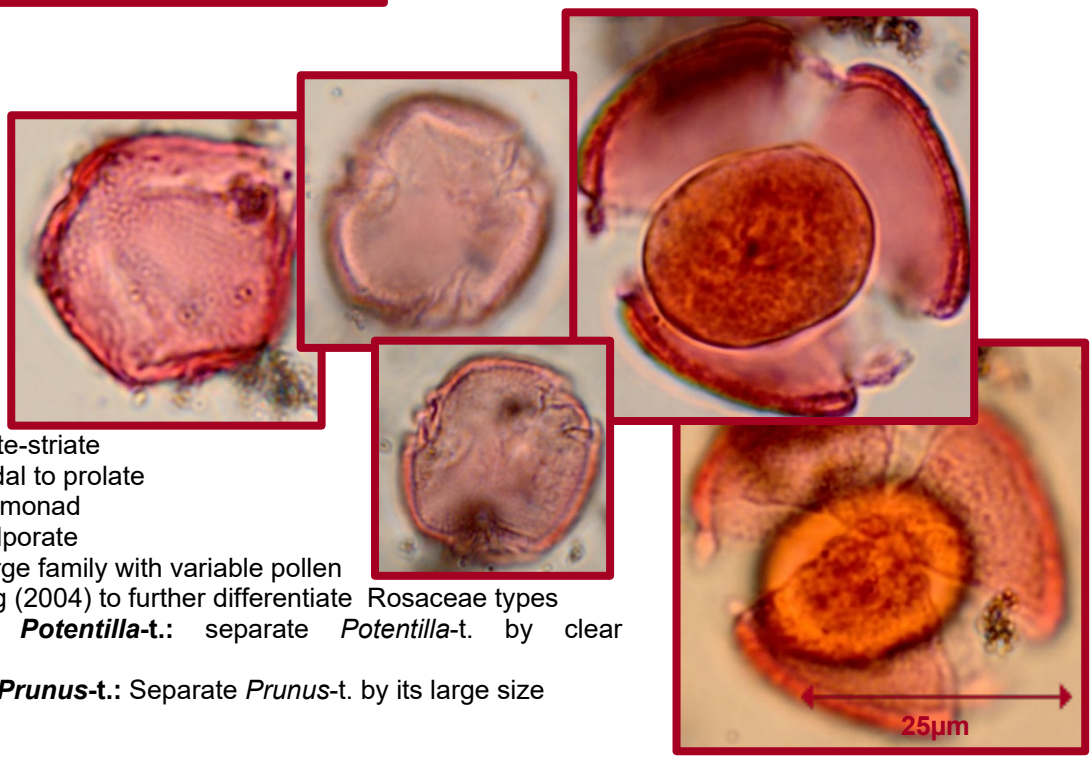
Helianthemum

Size: 30-60 µm
Structure: striate-reticulate
Shape: prolate, romboic shape
Dispersal unit: monad
Openings: tricolporate, round pores and long colpi



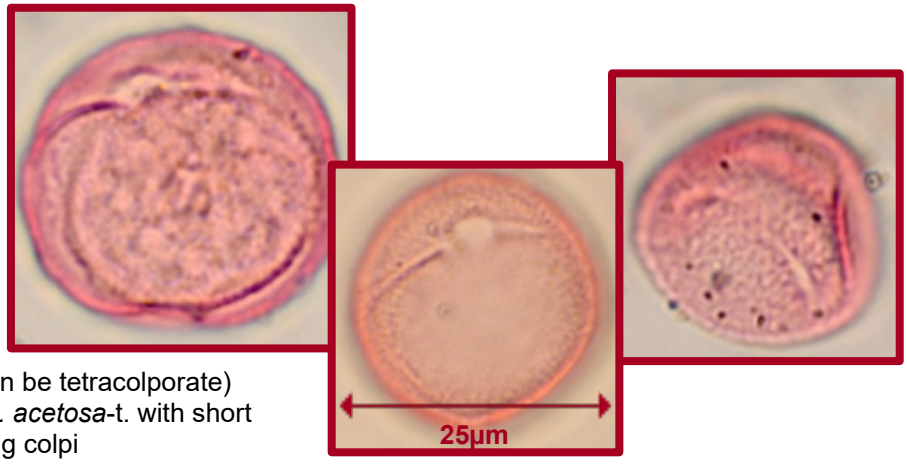
Rosaceae

Size: 15-40 µm
Structure: psilate-striate
Shape: spheroidal to prolate
Dispersal unit: monad
Openings: tricolporate
Other notes: large family with variable pollen Types, see Beug (2004) to further differentiate Rosaceae types
→**Differentiate *Potentilla*-t.:** separate *Potentilla*-t. by clear operculum
→**Differentiate *Prunus*-t.:** Separate *Prunus*-t. by its large size



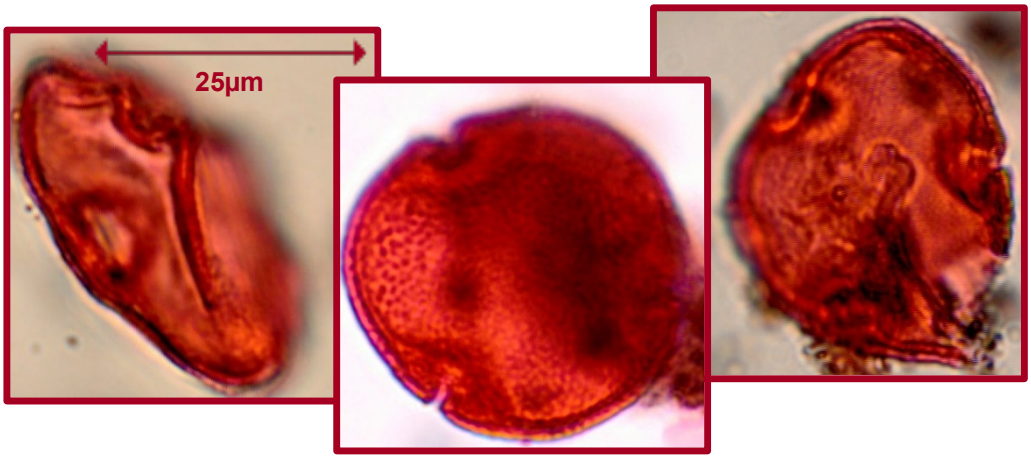
Rumex

Size: 18-35µm
Structure: microreticulate
Shape: spheroidal
Dispersal unit: monad
Openings: tricolporate (can be tetracolporate)
→**Differentiate *Rumex*:** *R. acetosa*-t. with short vs. *R. acetosella*-t. with long colpi



Tilia

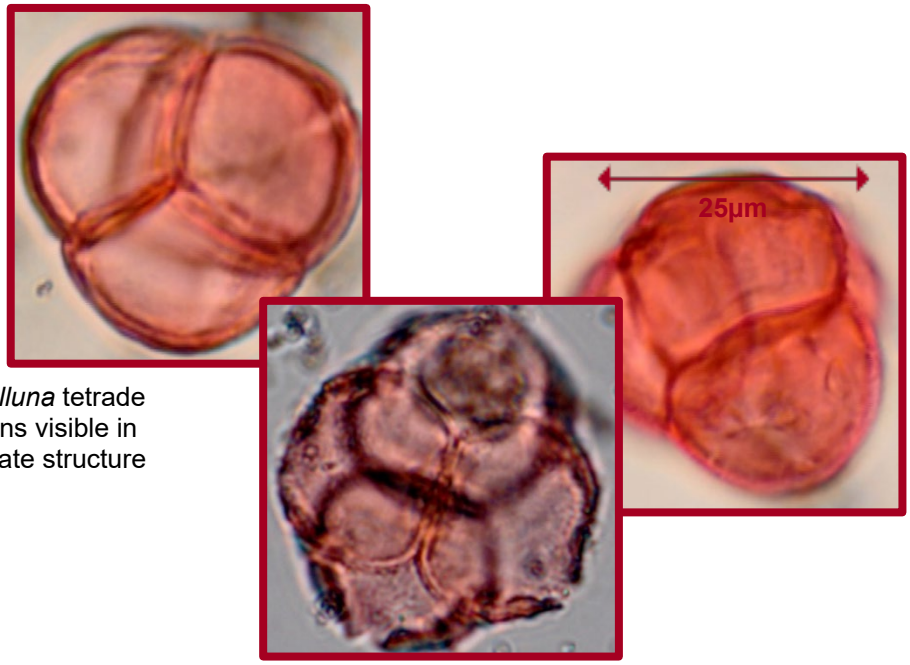
Size: 30-50 µm
Structure: faveolate-reticulate, very thick endexine around apertures
Shape: oblate
Dispersal unit: monad
Openings: tricolporate, very short colpi, can appear porate only



Tetrade pollen

Ericaceae

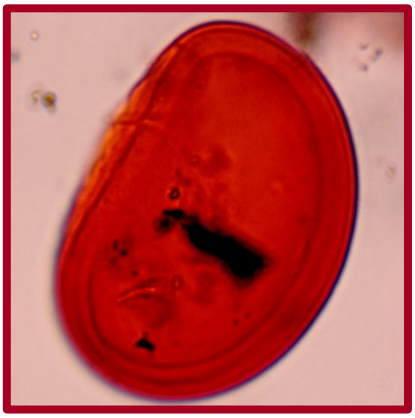
Size: 30-70 µm
Structure: psilate-scabrate
Shape: spheroidal
Dispersal unit: tetrade
Openings: colporate
→**Differentiate *Calluna***: *Calluna* tetrade often planar with all four grains visible in one view, scabrate to verrucate structure



Fern spores

Monolete fern spore

Size: 30-50 µm
Shape: bean-like shape
Dispersal unit: tetrade
Other notes: monolete tetrade mark



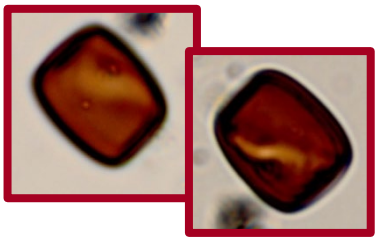
Trilete fern spore

Size: 30-50 µm
Shape: round or triangular shape
Dispersal unit: tetrade
Other notes: trilete tetrade mark

Fungal spores

Sporormiella

Size: 10 µm
Shape: square shape
Openings: one wave-shaped opening



Microscopic charcoal

Microscopic and macroscopic charcoal are an unambiguous tracer for biomass burning activity in the past (Tinner & Hu 2003). While macroscopic charcoal (>250µm) reflects fires of max. a few km distance (local signal, Adolf et al. 2018), microscopic charcoal can reach even remote regions and be deposited in polar ice archives. Microscopic charcoal can be counted alongside pollen and spores in microscopic slides.

Microscopic charcoal criteria for determination following Tinner & Hu (2003):

- Completely black and opaque,
- No metal shine even under polarized light,
- >10µm long, often elongated shape,
- Angular shape,
- Clear and straight edges.

→ Likewise, an item is **not to be counted** as microscopic charcoal if it is shiny, not completely black, if edges are rounded or if it is so small that criteria are not clearly visible!

Figure 4 Microscopic charcoal fragment under a light microscope.

Counting sums for microscopic charcoal following Finsinger & Tinner (2005):

- Minimum counting sums consist traditionally of 200 items (sum of charcoal fragments + Lycopodium spores)

→ Charcoal concentrations in ice are very low, so often only a few charcoal fragments are reached at a sum of 200. It is a good rule of thumb to continue until each group consists of minimum 20 items (i.e., 20 charcoal fragments + 180 *Lycopodium* spores).

Exercise to learn microscopic charcoal determination with light microscope in a few steps:

1. Burn a match in a petri dish
2. Lightly crush the generated charcoal fragments to small particles
3. Mix with a drop of glycerol
4. Mount on microscopic slide
5. Study the characteristics of microscopic charcoal particles under a light microscope

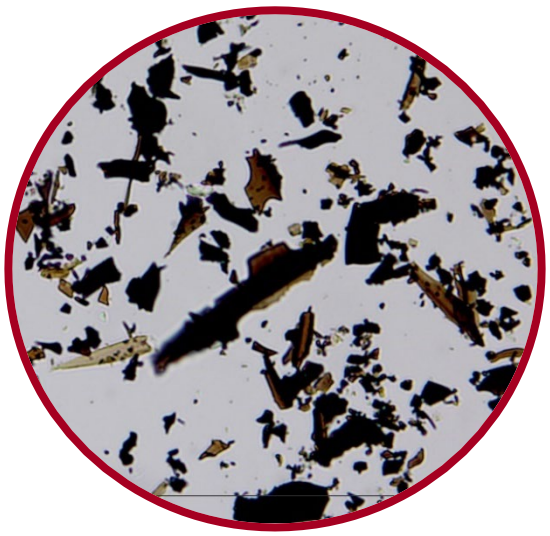


Figure 5 Microscopic charcoal particles from a burned match under a light microscope.

Acknowledgement

This manual is based on the workshop "Microfossils in Polar Ice - IPA Workshop Ice Palynology", 4.-5. April 2022 held at Desert Research Institute, Reno, Nevada. We are grateful to the University of Copenhagen for providing RECAP ice for the microfossil analyses of this project. We thank Aneeta Regi for her help with the microfossil pictures. We acknowledge funding from IPA (Internal Institute Project Assignments of Desert research Institute) grant awarded to Sandra O. Brugger.

References

Beug (2004) Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete. Pfeil, Munich.

Bourgeois (2000). Seasonal and interannual pollen variability in snow layers of arctic ice caps. Rev. Palaeobot. Palynol. 108(1-2), 17-36.

Bourgeois et al. (2000). A Holocene Ice-Core Pollen Record from Ellesmere Island, Nunavut, Canada. Quat. Res. 54, 275-283.

Brugger et al. (2018a). A quantitative comparison of microfossil extraction methods from ice cores. J. Glacial. 64(245), 432-442.

Brugger et al. (2018b). Ice records provide new insights into climatic vulnerability of Central Asian forest and steppe communities. Global Planet. Change 169, 188-201.

Brugger et al. (2019a). Palynological insights into global change impacts on Arctic vegetation, fire, and pollution recorded in Central Greenland ice. Holocene 29(7), 1189-1197.

Brugger et al. (2019b). Tropical Andean glacier reveals colonial legacy in modern mountain ecosystems. Quat. Sci. Rev. 220, 1-13.

Brugger et al. (2019c). Why loss matters: Reply to the comments of Festi and others on 'A quantitative comparison of microfossil extraction methods from ice cores' by Brugger and others (2018). J. Glaciol. 65(253), 867-868.

Brugger et al. (2021). Alpine glacier reveals ecosystem impacts of Europe's prosperity and peril over the last millennium. Geophys. Res. Lett. 48(20), e2021GL095039.

Brugger et al. (in press). High-latitude fire activity of recent decades derived from microscopic charcoal and black carbon in Greenland ice cores. Holocene, accepted.

Clegg et al. (2005). Morphological differentiation of Betula (birch) pollen in northwest North America and its palaeoecological application. Holocene 15(2) 229-237.

Eichler et al. (2011). An ice-core based history of Siberian forest fires since AD 1250. Quat. Sci. Rev. 30(9-10), 1027-1034.

Feurdean et al. (2011). Evaluating the palaeoecological potential of pollen recovered from ice in caves: A case study from Scărişoara Ice Cave, Romania. Rev. Palaeobot. Palyno. 165(1-2), 1-10.

Finsinger & Tinner (2005). Minimum count sums for charcoal concentration estimates in pollen slides: accuracy and potential errors. Holocene 15(2), 293-297.

Fredskild & Wagner (1974). Pollen and fragments of plant tissue in core samples from the Greenland ice cap. Boreas 3(3), 105-108.

Heiri & Lotter (2001). Effect of low count sums on quantitative environmental reconstructions: an example using subfossil chironomids. J. Paleolimnol. 26(3), 343-350.

Hicks & Isaksson (2006). Assessing source areas of pollutants from studies of fly ash, charcoal, and pollen from Svalbard snow and ice. J. Geophys. Res. Atmos. 111(D2).

Koerner et al. (1988). Pollen analysis and discussion of time-scales in Canadian ice cores. Ann. Glaciol. 10, 85-91.

Lang (1994). Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse. Springer.

Leunda et al. (2019). Ice cave reveals environmental forcing of long-term Pyrenean tree line dynamics. J. Ecol. 107(2), 814-828.

Liu et al. (1998). A pollen record of Holocene climatic changes from the Dunde ice cap, Qinghai-Tibetan Plateau. Geology 26(2), 135-138.

Liu et al. (2005). Ice-core pollen record of climatic changes in the central Andes during the last 400 yr. Quat. Res. 64(2), 272-278.

Liu et al. (2007). A potential pollen proxy for ENSO derived from the Sajama ice core. Geophys. Res. Lett. 34(9).

Manten (1966). Half a century of modern palynology. Earth-Sci. Rev. 2, 277-316.

Moore et al. (1991). Pollen analysis. Blackwell Scientific, 2nd edition, Oxford.

Nakazawa & Fujita (2006). Use of ice cores from glaciers with melting for reconstructing mean summer temperature variations. Ann. Glaciol. 43, 167-171.

Nakazawa et al. (2004). Application of pollen analysis to dating of ice cores from lower-latitude glaciers. J. Geophys. Res. Earth Surf. 109(F4).

Nakazawa et al. (2005). Dating of seasonal snow/firn accumulation layers using pollen analysis. J. Glaciol. 51(174), 483-490.

PalDat – a palynological database (2000 onwards, www.paldat.org)

Reese & Liu (2002). Pollen dispersal and deposition on the Quelccaya Ice Cap, Peru. Phys. Geogr. 23(1), 44-58.

Reese et al. (2003). Pollen dispersal and deposition on the ice cap of Volćan Parinacota, Southwestern Bolivia. Arctic Antarc. Alp. Res. 35(4), 469-474.

Rey et al. (2019). Causes and mechanisms of synchronous succession trajectories in primeval Central European mixed Fagus sylvatica forests. J. Ecol. 107(3), 1392-1408.

Short & Holdsworth (1985). Pollen, oxygen isotope content and seasonally in an ice core from the penny Ice Cap, Baffin Island. Arctic 214-218.

Stockmarr (1971). Tabletes with spores used in absolute pollen analysis. Pollen spores, 13, 615-621.

Tinner & Hu (2003). Size parameters, size-class distribution and area-number relationship of microscopic charcoal: relevance for fire reconstruction. Holocene, 13(4), 499-505.

Yang et al. (2008). Summer temperature reconstruction on the central Tibetan Plateau during 1860–2002 derived from annually resolved ice core pollen. J. Res. Atmos. 113(D24).