Misinterpretations in Palynology

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The description of pollen ornamentation depends on three major parameters (1) the interpretations of the palynologist (which are subjective), (2) the pollen terminology applied, and (3) the magnification, resolution, and methods used.

The application of different preparation and staining methods and a combined analysis with light microscopy, scanning- and transmission electron microscopy are essential for the interpretation of pollen characters. Investigation of recent and fossil pollen material often reveals interesting features that in some cases may be misinterpreted. To demonstrate the wide range of possible misinterpretations, the following examples are given:

Example 1: Tripartite Feature in Gymnosperms — Impression Mark

Mature pollen of conifers, such as *Abies*, *Larix*, and *Pseudotsuga,* often shows proximally a Y-shaped bulge on the proximal polar side, comparable to a tetrad mark, which is called an **impression mark** (Fig. 1; Harley 1999). The mark results from the close proximity of the four pollen grains at the post-meiotic tetrad phase and is retained afterwards and is not a germination feature. Impression marks are also found in palm pollen. Note: the term tetrad mark is restricted to spores, where it is a germination feature.

Example 2: Tripartite Feature in Angiosperms — Triangular Tenuitas

Superficially similar features in angiosperms are not comparable to those observed in gymnosperms. In recent and fossil Sapindaceae a three-armed feature (more precisely a triangle) is found. *Cardiospermum* has a narrow **triangular tenuitas** (thinning) at the proximal pole, whereas other recent and subfossil Sapindaceae show such a feature at both poles (Fig. 2).

Example 3: Tripartite Feature in Angiosperms — Synaperture

Triangular pollen as found in Myrtaceae, some Primulaceae (*Primula farinosa* or *P. denticulata*) and Loranthaceae is characterized by a tripartite feature in both polar areas (Fig. 3). These are in fact

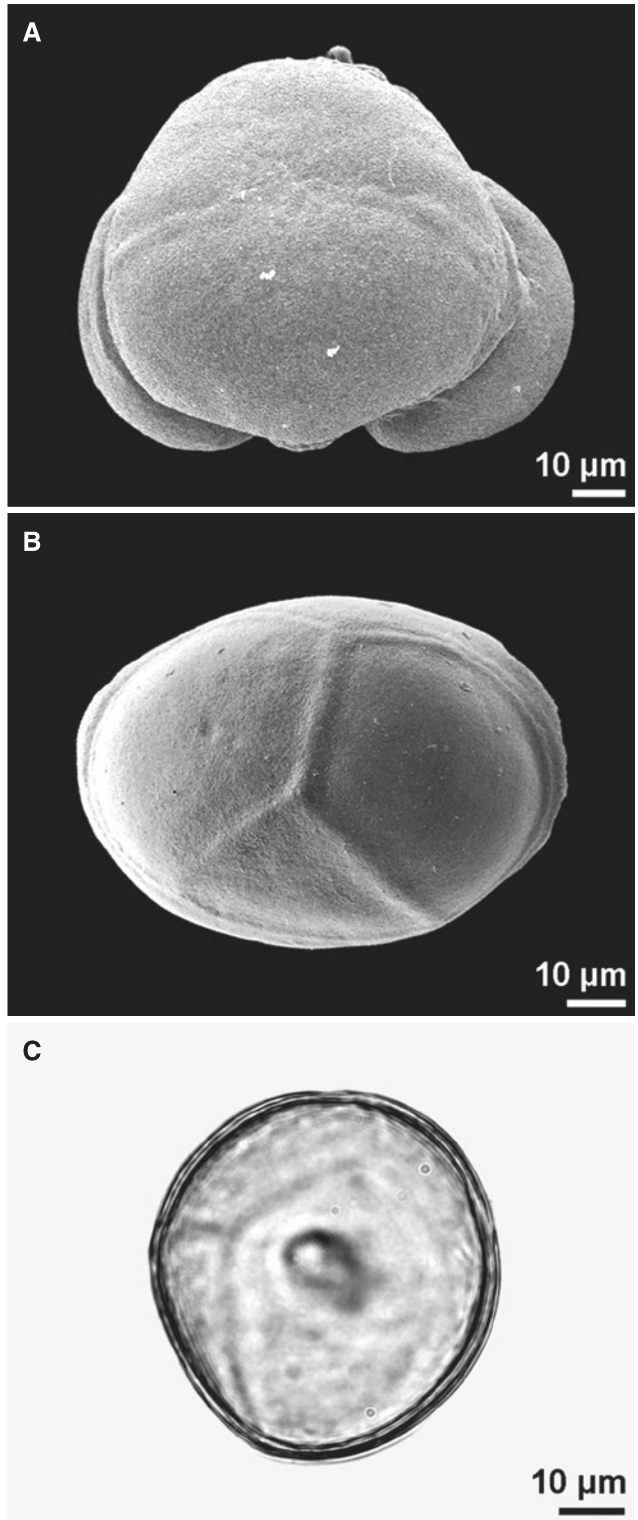

Fig. 1 Impression mark. **A.** *Abies cephalonica*, Pinaceae, proximal polar view, indistinct impression mark. **B-C.** *Larix* sp., Pinaceae, fossil, middle Miocene, Austria, proximal polar view, Y-shaped impression mark in SEM (**B**) and LM (**C**)

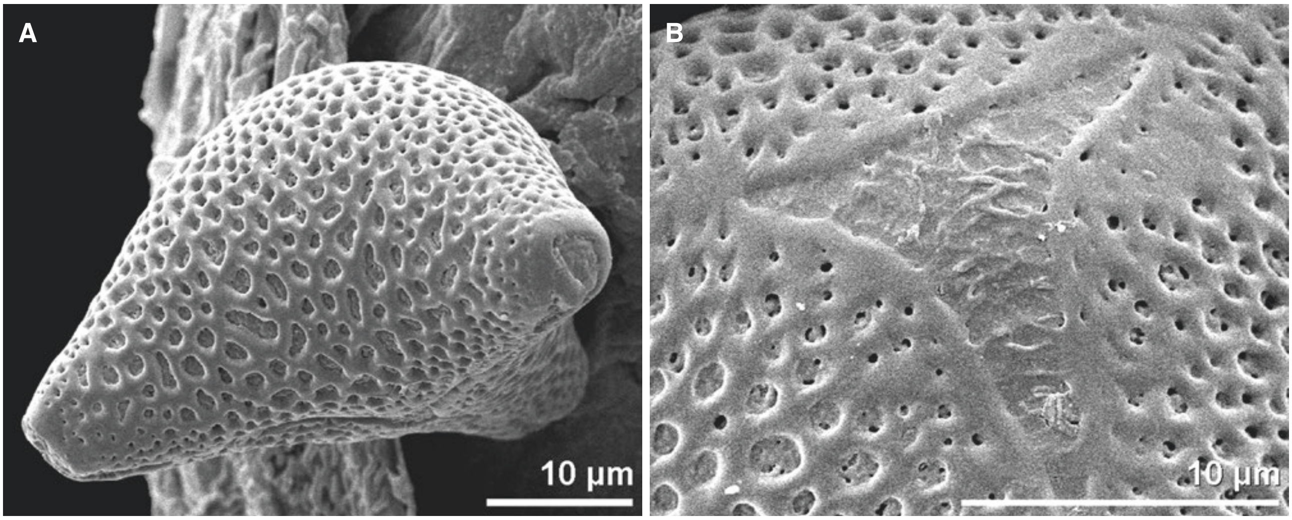

Fig. 2 Triangular tenuitas. **A-B.** *Cardiospermum corindum*, Sapindaceae, tricolporate, equatorial view (**A**), proximal pole with triangular thinning area (**B**)

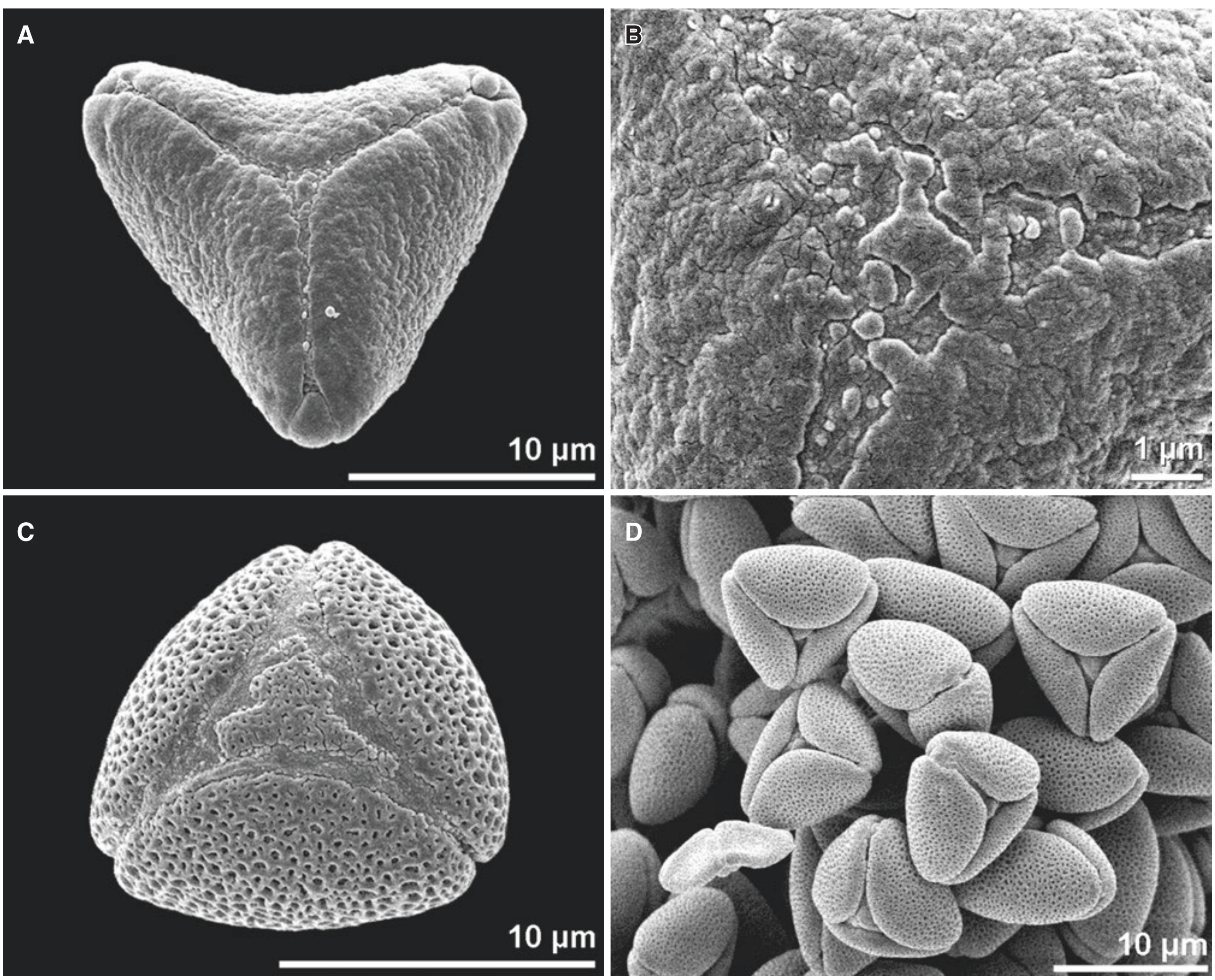

Fig. 3 Synaperturate pollen. **A-B.** *Melaleuca armillaris*, Myrthaceae, syncolporate, polar view (**A**), close-up of polar area (**B**). **C.** *Primula denticulata*, Primulaceae, syncolpate, polar view. **D.** *Primula farinosa*, Primulaceae, syncolpate, dry pollen

three colpi, extending towards and merging at the poles. The pollen is therefore synaperturate (syncolpate, syncolporate). In for example, *Primula* the colpi dissect in the polar area, leaving a triangular field at both poles.

Example 4: Tripartite Feature in Angiosperms — Trichotomosulcus

Another tripartite feature is the **trichotomosulcus** (Harley 2004), a three-armed sulcus occurring exclusively distally, as, e.g., in *Dianella*. Trichotomosulcate pollen has been discussed in relation to the evolution of the tricolpate dicot condition, but so far without success (Fig. 4).

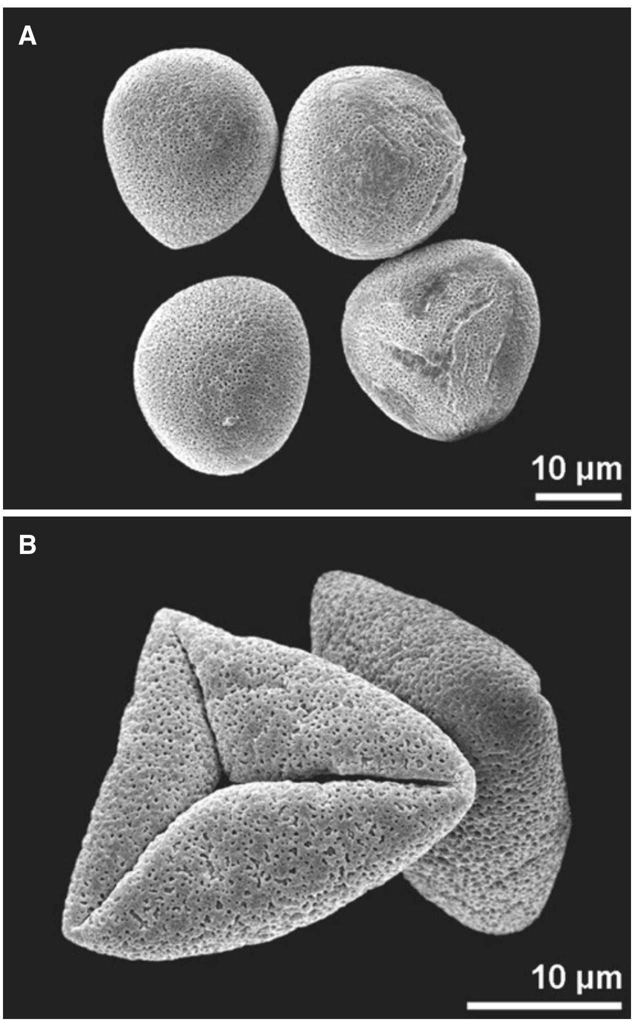

Fig. 4 Trichotomosulcus. **A-B.** *Dianella tasmanica*, Phormiaceae, trichotomosulcus (**A**), dry pollen, aperture infolded (**B**)

Example 5: Tripartite Feature in Angiosperms — Sulci vs. Colpi vs. Tenuitas

The angiosperm-like pollen of the fossil genus *Eucommiidites* is "trisulcate": a broad distal sulcus and two narrower additional "sulci" (at angles of c. 120° seen from the main sulcus; Fig. 5). This feature was erroneously interpreted as tricolpate pollen (with colpi equatorially situated).

A similar arrangement of a distal sulcus and two small additional sulci on the proximal face was described, for example, in some species of *Tulipa* (Liliaceae) and *Tinantia* (formerly *Commelinantia*, Commelinaceae), but these cases were never interpreted as equivalent to a tricolpate condition (Harley 2004) (Fig. 6). The two small additional sulci may also be interpreted as tenuitates. In some cases the three "sulci" are of similar size. The aperture condition is very similar to a tricolpate one.

Example 6: Tripartite Feature in Angiosperms — Triradiate Aperture

Another three-armed feature is the triradiate aperture in *Thesium alpinum* (Santalaceae) pollen. The heteropolar pollen is 3-aperturate, with apertures placed in the three tapered edges of a tetrahedron (Feuer 1977). Each aperture has a very inconspicuous triradiate outline, which is situated equatorially. Two of the arms point towards the neighboring tetrahedron edge and are rather short; the third, elongated arm is directed towards the rounded pole (Fig. 7).

Example 7: Apertures in Angiosperms — Planaperturate

Sometimes apertures are inconspicuous and not discernible at first sight. In pollen of *Pachira aquatica* (Malvaceae) three large, more-or-less hemispherical areas are seen equatorially, which may at first sight be interpreted as pores. However, a detailed observation reveals **planaperturate** pollen grains with three short colpi (Fig. 8).

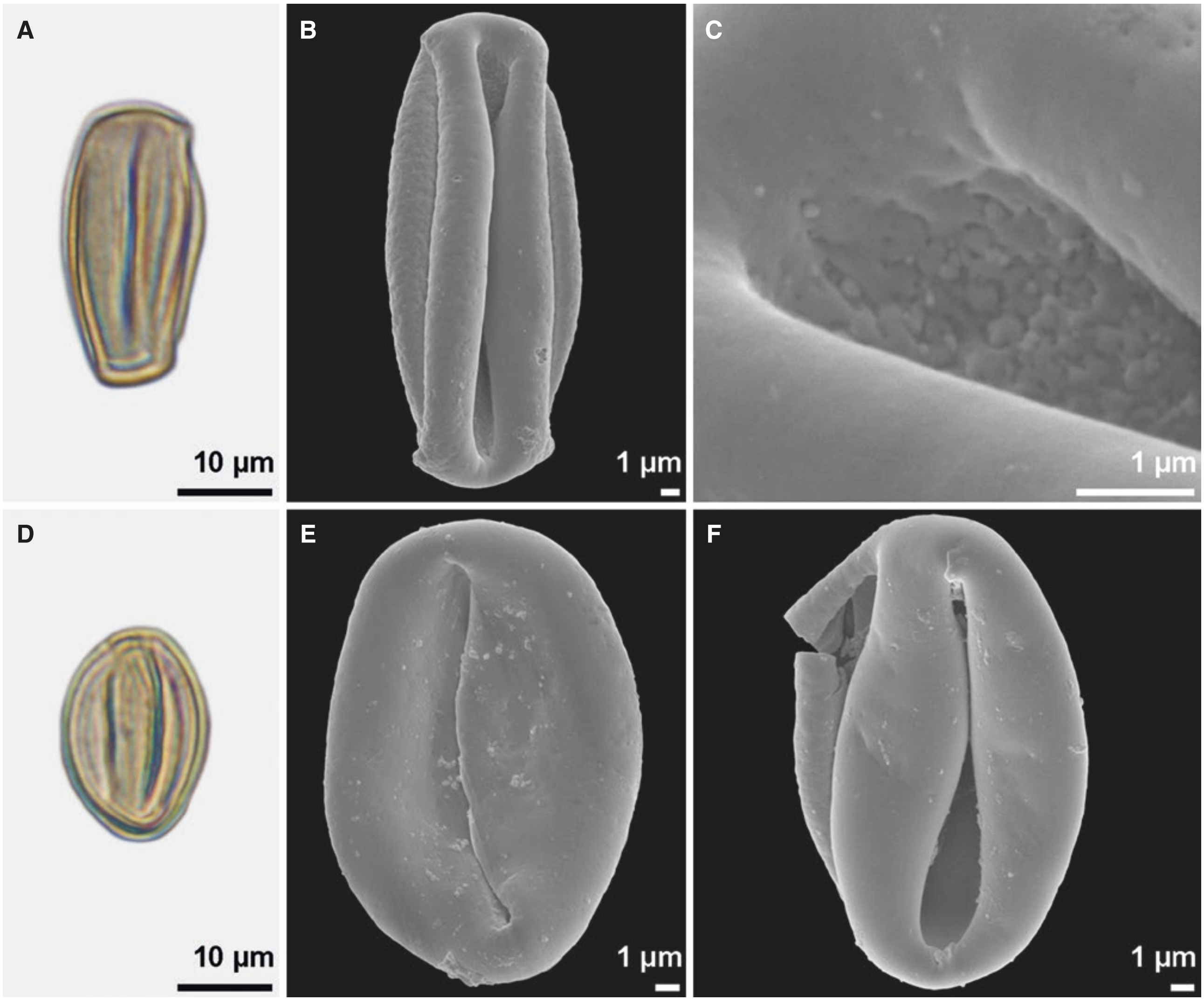

Fig. 5 Trisulcate pollen. **A-C.** *Eucommiidites* sp., fossil pollen, Lower Cretaceous of U.S.A., main sulcus with membrane seen in center of pollen grain, flanked by additional narrow sulci on each side (at angles of c. 120°, **A-B**), close-up showing sulcus membrane of main sulcus (**C**). **D-F.** *Eucommiidites* sp., fossil pollen, Lower Cretaceous of U.S.A., Narrow lateral sulcus (**E**), same grain turned showing the main broad sulcus and one narrow lateral sulcus (**F**)

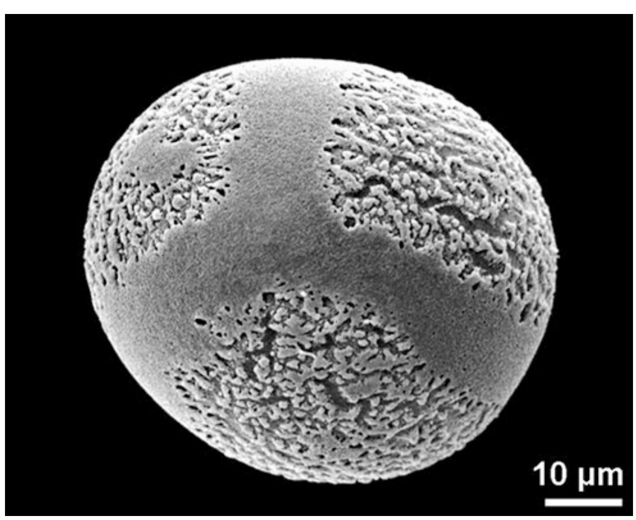

Fig. 6 Trisulcate pollen. *Tulipa kaufmanniana*, Liliaceae, trisulcate or sulcate with two tenuitates, equatorial view

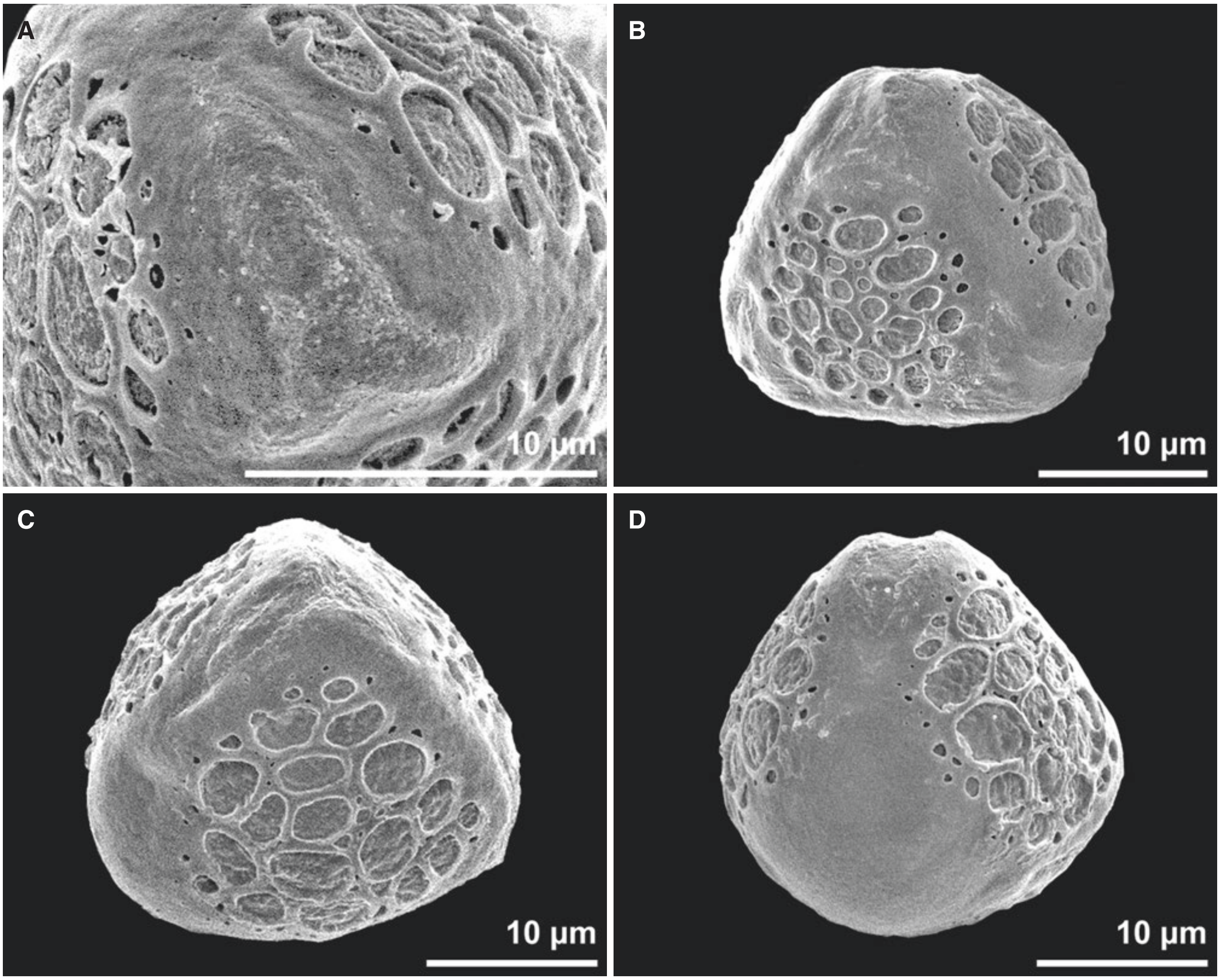

Fig. 7 Triradiate aperture. **A-D.** *Thesium alpinum*, Santalaceae. **A.** Tricolpate, heteropolar, triradiate colpus. **B.** Polar view (flattened pole). **C.** Equatorial view. **D.** Polar view (rounded pole)

Example 8: Apertures in Angiosperms — Inconspicuous Pori

In *Calliandra emarginata* (Mimosaceae) the monads forming a polyad are separated by narrow groove-like depressions. At low magnification the presence and localization of the apertures remain indistinct; high SEM magnification reveals that the apertures are very inconspicuous pores, situated equatorially, usually at the conjunction of three or four monads (Fig. 9 A, B).

Also, the aperture condition may be overlooked due to other eye-catching features. The clypeate pollen of *Phyllanthus* x *elongatus* (Euphorbiaceae) seems to be inaperturate. Only close-ups reveal the inconspicuous few pores between the exine shields (Fig. 9 C, D).

Example 9: Apertures in Angiosperms — Inconspicuous Colpi

The disc-like pollen of *Oryctanthus* sp. (Loranthaceae) shows at both poles conspicuous circular depressions that are not apertures (Feuer and Kuijt 1985; Grímsson et al. 2018). The pollen is according to Grímsson et al. (2018) demi(3)colpate, with

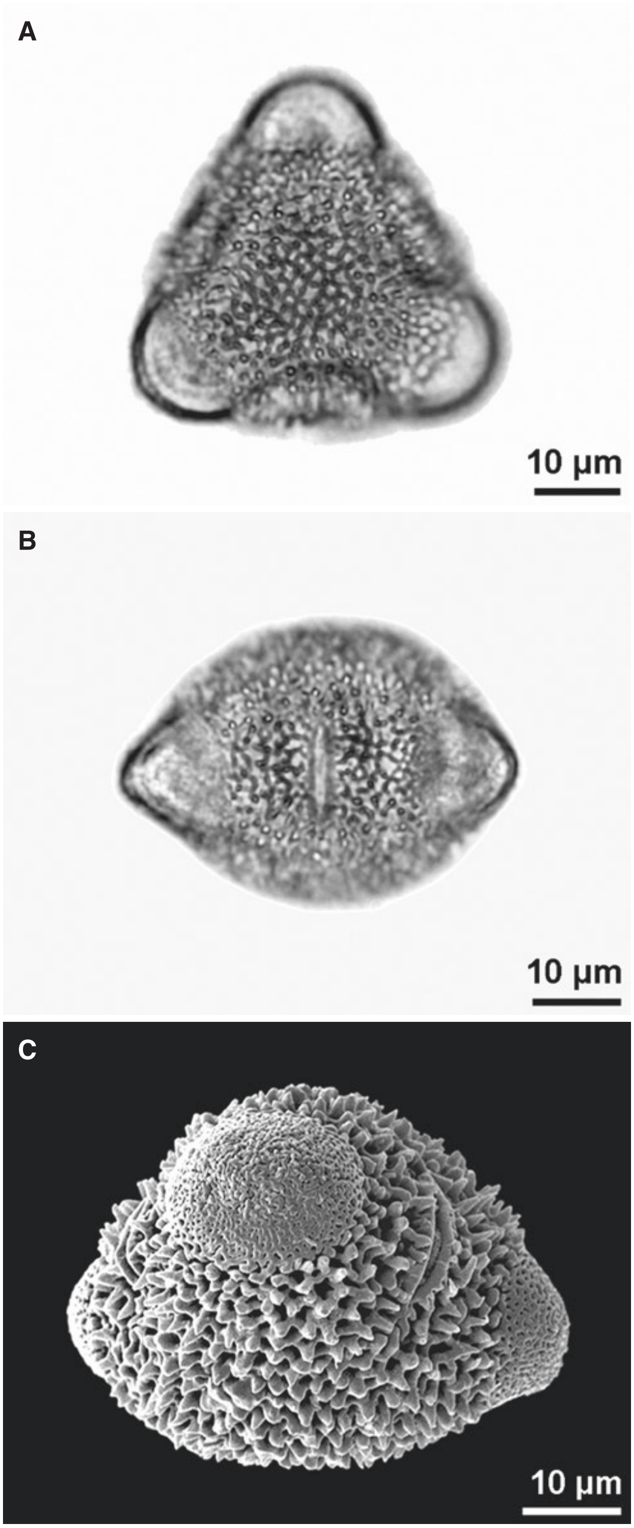

Fig. 8 Planaperturate pollen. **A-C.** *Pachira aquatica*, Malvaceae, polar view (**A**), equatorial view (**B**), oblique equatorial view (**C**)

inconspicuous slit-like colpi positioned between the polar depressions (Fig. 10). Another example are some Asteraceae pollen, where the colpi are often inconspicuous or not visible in SEM, but obvious in LM.

Example 10: Apertures in Angiosperms — Hidden Apertures

Recent and fossil triaperturate (colpate or porate) pollen of *Trapa* (Trapaceae) is distinguished by unique meridional exine ridges (crests) covering the apertures (Zetter and Ferguson 2001) (Fig. 11).

Example 11: Apertures in Angiosperms — Ring-like Apertures vs. Colpate-Operculate

The apertures in *Passiflora* cf. *incarnata* may be interpreted as three ring-like apertures or may be interpreted as pori (or colpi) each with an operculum. In other species of *Passiflora* e.g., *P. citrina* and *P. suberosa*, the apertures are both narrower and stephanocolpate (Fig. 12).

Example 12: Apertures in Angiosperms — Tenuitas vs. Poroid

Tenuitas is a general term for a pollen wall thinning (Kremp 1968; Harley 2004; Punt et al. 2007). It is normally found additional to apertures, e.g., in *Myosotis* (Fig. 13). A circular tenuitas can be mistaken for a **poroid**, which is a circular or elliptic aperture with an indistinct margin (see also "Illustrated Pollen Terms").

Example 13: Apertures in Angiosperms — Infoldings vs. Apertures

When pollen is infolded it can be hard to distinguish the apertures. Pollen of *Sparganium erectum* (Sparganiaceae) is in dry stage infolded, boat-shaped, and would be considered as sulcate. In fact, *Sparganium* pollen is ulcerate, the ulcus is seen clearly in the hydrated, spherical pollen stage (Fig. 14).

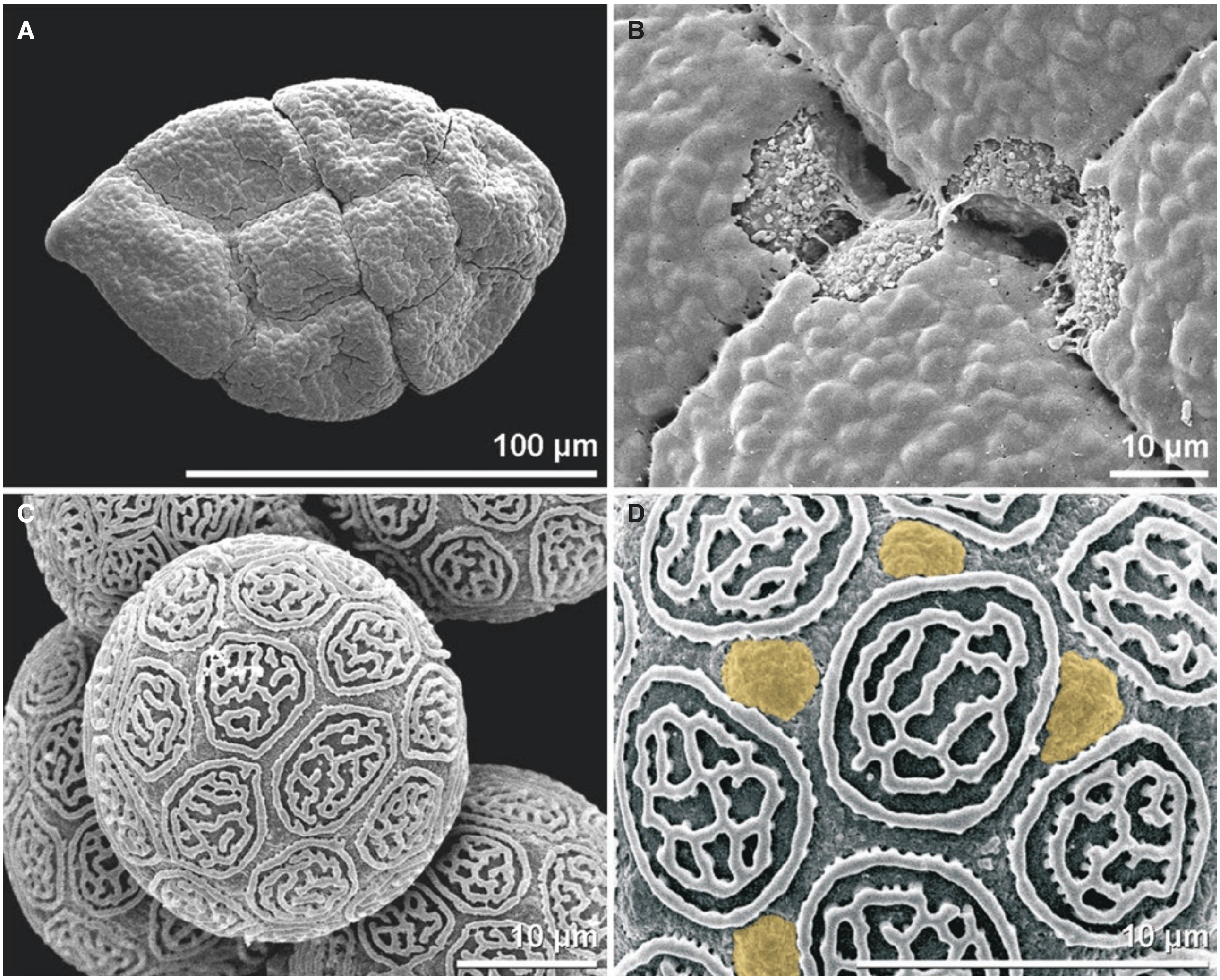

Fig. 9 Apertures in *Calliandra* and *Phyllanthus*. A-B. *Calliandra tergemina*, Fabaceae, polyad, dry state (**A**). Apertures (pori) at the junction of four monads (**B**). **C-D.** *Phyllanthus x elongatus*, Euphorbiaceae, clypeate, seemingly inaperturate (**C**), Inconspicuous pores (colored) between the exine shields (**D**)

Example 14: Apertures in Angiosperms — Ulcerate-Operculate vs. Ring-like Aperture

Nymphaea alba (Nymphaeaceae) pollen has asymmetrical halves divided by a ring-like aperture (Fig. 15). The features of the smaller distal half may be misinterpreted as a large ulcus with a conspicuous operculum. Ultrastructural studies and germination experiments support the interpretation of a ring-like aperture (Gabarayeva and Rowley 1994; Hesse and Zetter 2005).

Example 15: Apertures in Angiosperms — Disulcate vs. Dicolpate

The term disulcate defines two elongated apertures situated usually distally (but not directly at the distal pole), running parallel to or even in the equator (Fig. 16). If the apertures are running meridionally, pollen would be dicolpate (Halbritter and Hesse 1993). To distinguish if the pollen is disulcate or dicolpate it is important to study the pollen in tetrad arrangement to clarify the polarity and position of apertures (see Fig. 3 in "Methods in Palynology").

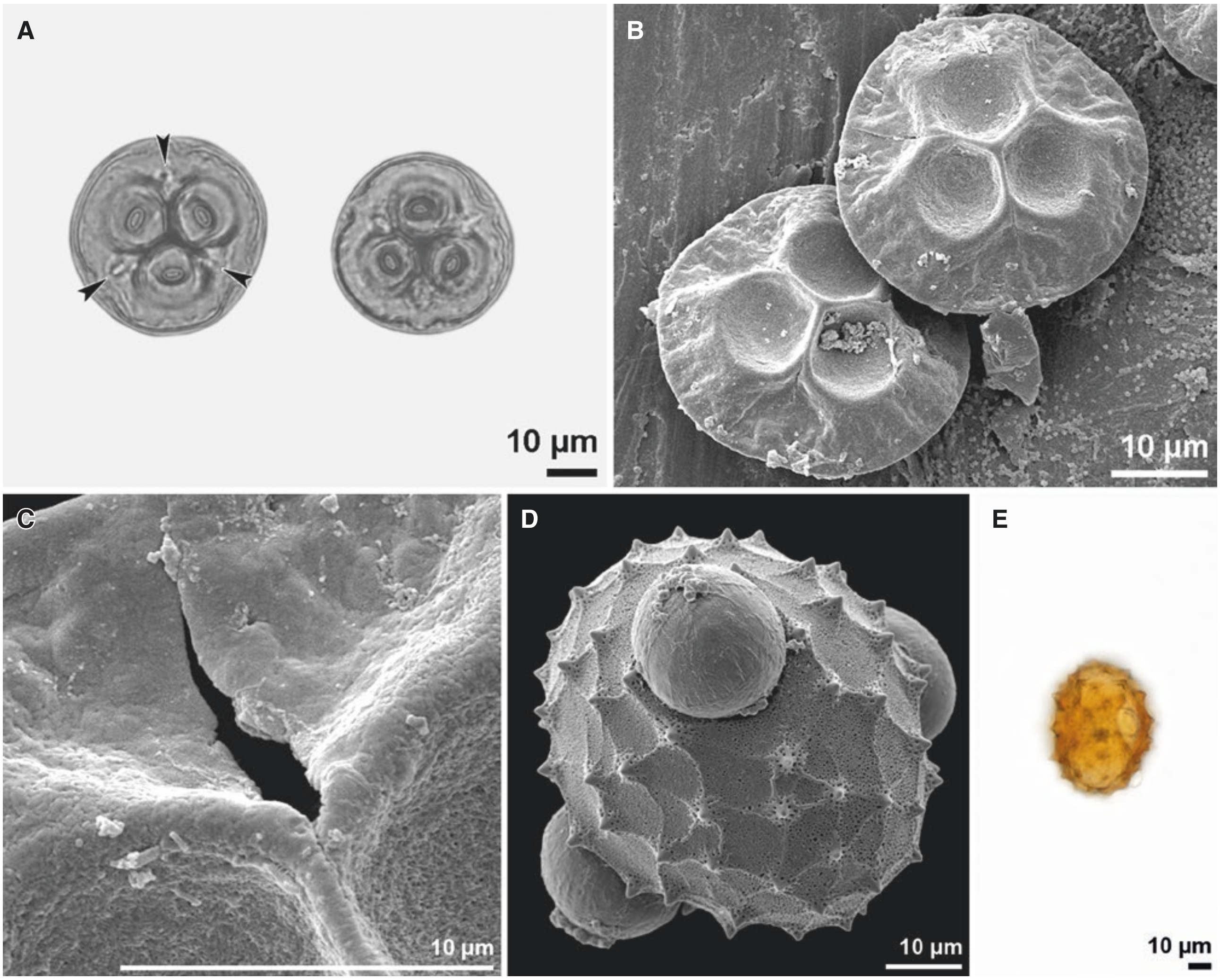

Fig. 10 Apertures in *Oryctanthus*. A-C. *Oryctanthus alveolatus*, Loranthaceae, acetolyzed pollen, arrowheads point to colpi, LM (**A**). two grains in polar view, SEM (**B**). close-up showing colpus (**C**). **D-E.** *Carthamus lanatus*, Asteraceae, hydrated pollen, pollen in SEM seem porate (**D**). Acetolyzed pollen, colporus (highlighted) only visible in LM (**E**)

Examples for taxa with disulcate pollen are the monocots *Tofieldia calyculata* with one sulcus distally, the other proximally, *Uvularia grandiflora*, *Eichhornia crassipes* (Hesse et al. 2009), some *Dioscorea* species (Schols et al. 2005), *Pontederia cordata* (Halbritter 2016), *Calla palustris* (Ulrich et al. 2013), and the magnoliid *Calycanthus floridus* (Huynh 1976).

Example 16: Apertures in Angiosperms — Zon-, Zono-, Zoni-, Zona- vs. Ring-like Aperture and Stephanoaperturate Pollen

Terms combining the basic prefix zon- together with its linguistic derivatives are a source of endless confusion, misunderstanding and superfluous inflation of terms. The prefix include **zon-** (in zonorate, for a ring-like endoaperture, the os, at the equator), the outdated, rarely used **zoni-** (however, with two quite different terminological applications), but especially **zona-** (indicating exclusively a ring-like feature situated anywhere) and **zono-** (indicating any feature located strictly equatorially).

Terms for ring-like (aperture) features include zona-aperturate, zona-sulculus (addressing the polarity by anazona-sulculus and catazona-sulculus), zona-sulcus, zonate, zono-aperturate, and also related names (e.g., "fully zonate condition" sensu Grayum 1992). Even the misleading and contradictory **zono**-sulcus (a sulcus cannot be situated equatorially) is used instead of the correct, but phonetically confusable, **zona**-sulcus. Even the

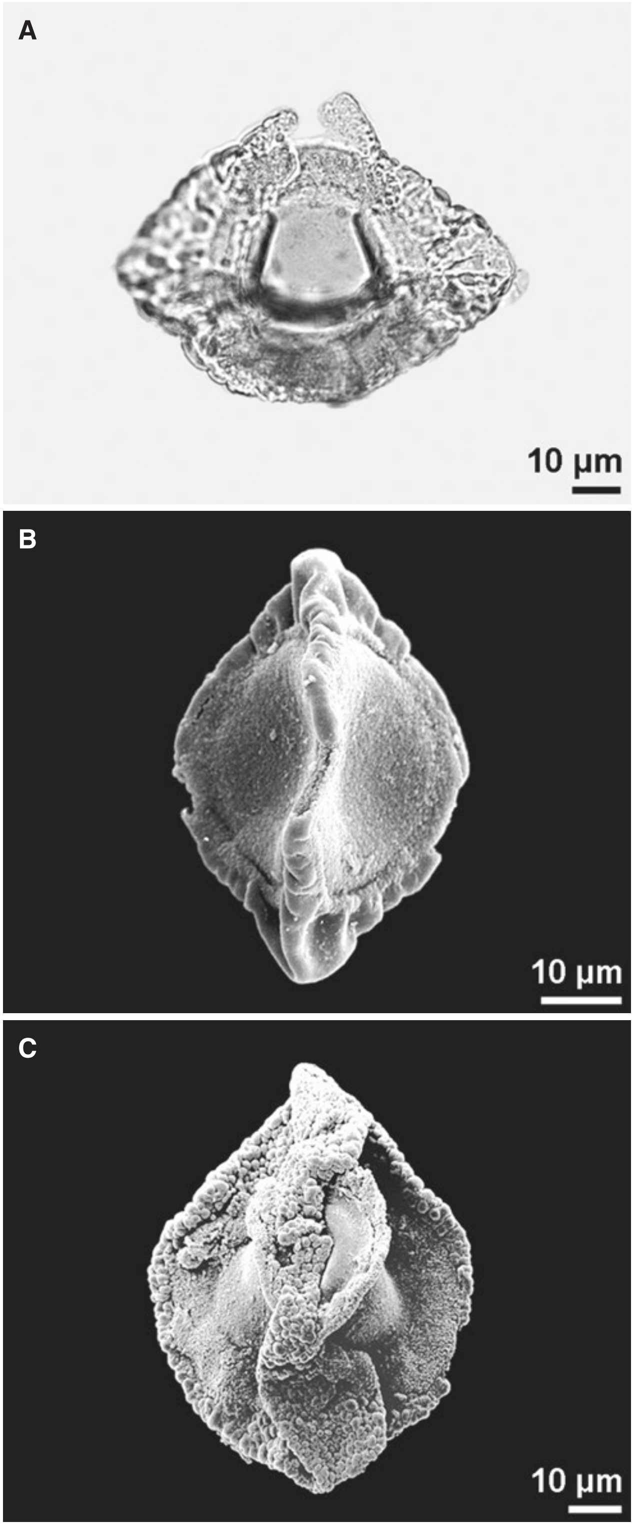

Fig. 11 Apertures in *Trapa*. A-C. *Trapa* sp., Trapaceae, fossil, late Miocene, Austria, equatorial view, crest broken, LM (**A**). Equatorial view, crest partly broken, colpus visible in SEM (**B**). Equatorial view, SEM (**C**)

trained palynologist may become confused. Therefore, all these terms should be avoided and we recommend the following two terms: **ring-like aperture and stephanoaperturate** (see "Illustrated Pollen Terms"). Any encircling aperture ("zona-aperturate"), irrespective of meridional or equatorial location, is simply called a **ring-like aperture**. Any case with more than three apertures at the equator ("zono-aperturate") is called **stephanoaperturate**.

Example 17: Magnification Effect — Retipilate vs. Reticulum Cristatum

The term retipilate (reticuloid) describes a reticulum formed by pila instead of muri (Erdtman 1952). Combined investigations based on LM and SEM have revealed that the given examples *Callitriche* (Punt et al. 2007) and *Cuscuta lupuliformis* (Erdtman 1952) do not fit the definition of retipilate. In fact, the reticulum consists of muri with prominent suprasculpture elements and are without isolated pilae. Such ornamentation is termed reticulum cristatum (a special type of reticulum; muri with prominent suprasculpture elements; Fig. 17, see also "Illustrated Pollen Terms"). So far no example for retipilate sensu Erdtman (1952) is currently known.

Example 18: Dispersal Units — Massula vs. Polyad

For a pollen dispersal unit of more than four pollen grains two terms are in use, **massula** and **polyad** (Fig. 18). The application of both terms is confusing and inconsistent in the literature. Often, the various authors employ the terms more or less interchangeably and do not provide a sharp delimitation (Walker 1971; Wagenitz 2003; Punt et al. 2007; Traverse 2007). These terms, however, are not exchangeable for historical and practical reasons (see extensive review by Teppner 2007).

The term massula was coined by Richard (1817) for parts of a pollinium in some Orchidaceae and should be used for the subunits of orchid sectile pollinia/pollinaria. Massulae within one and the same pollinium are variable and different in shape, size, and numbers of pollen grains. Unfortunately, the term massula has also been used to designate compound pollen in various other families, e.g.

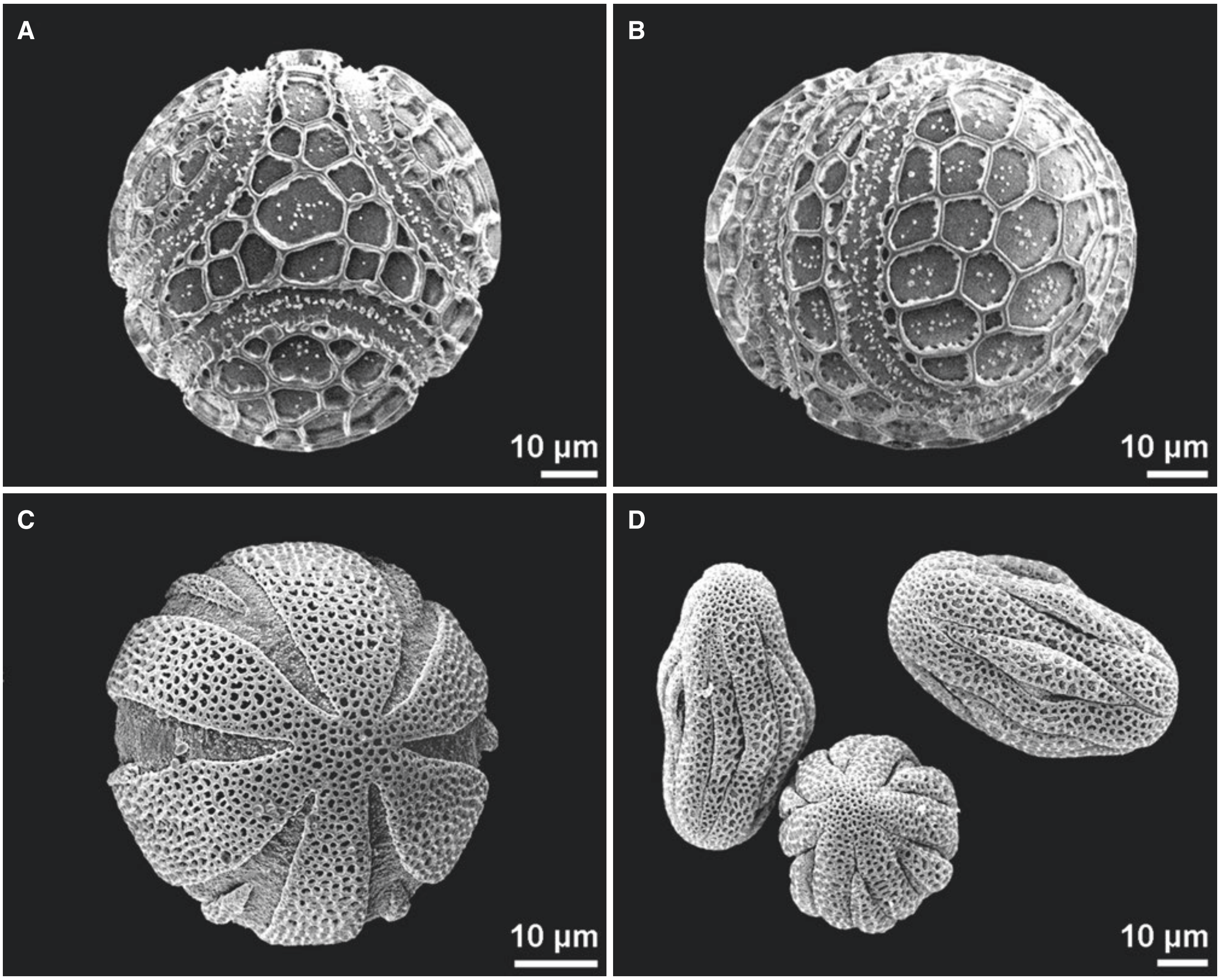

Fig. 12 Apertures in *Passiflora*. A-B. *Passiflora* cf. *incarnata*, Passifloraceae; colpate, operculate aperture, polar view (**A**), equatorial view (**B**). **C.** *Passiflora citrina*, Passifloraceae, stephanocolpate, operculate, polar view. **D.** *Passiflora suberosa*, Passifloraceae, stephanocolpate, operculate, dry pollen

Fabaceae-Mimosoideae, producing dispersal units of more than four pollen grains (e.g., Wettstein 1907; Wagenitz 2003; Punt et al. 2007). For these the term polyad — coined by Iversen and Troels-Smith (1950) — should be used, denoting a symmetric dispersal unit of more than four regularly arranged and permanently united pollen grains. Polyads, currently known to occur in Fabaceae (Mimosoideae), Gentianaceae, Hippocrateaceae, Celastraceae and Annonaceae, contain a specific number of pollen grains (a multiple of four: 8, 12, 16, 24, 32, 48, 64) and show a species-specific shape.

Example 19: Preparation Effect — Psilate vs. Ornamented

Ornamentation sometimes depends on the **preparation method**. A striking example is pollen of many Aroideae (Araceae), that are ornamented (e.g., echinate, striate, verrucate) in fresh or dry condition, but become psilate following acetolysis (Fig. 19). The outer pollen wall layer and ornamentation elements are composed of polysaccharide (lack sporopollenin) and are therefore destroyed during acetolysis (Weber et al. 1999; Ulrich et al. 2017).

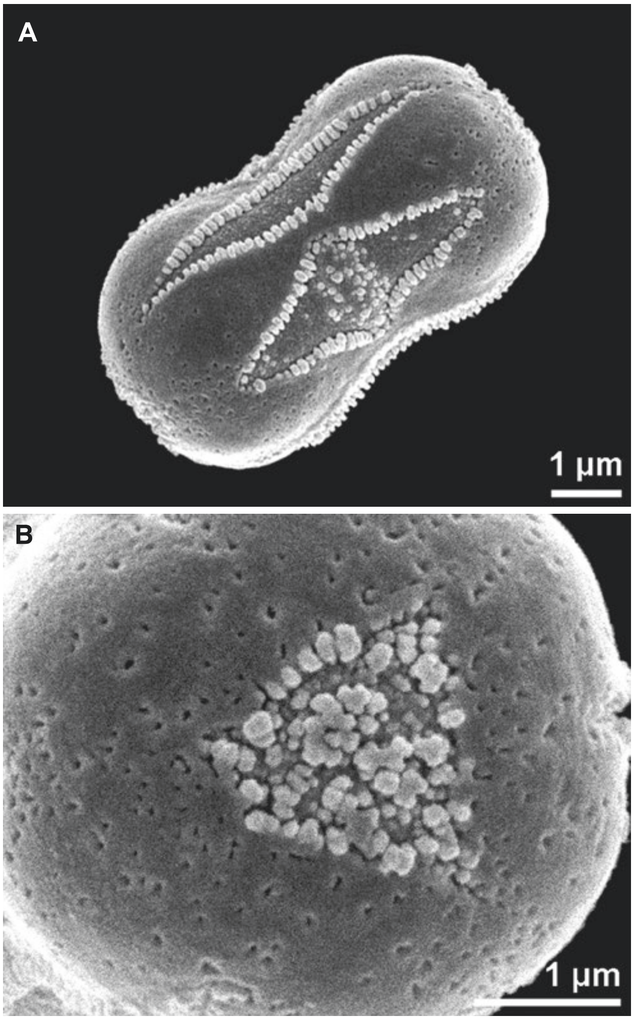

Fig. 13 Tenuitas vs. poroid. **A-B.** *Myosotis palustris*, Boraginaceae, equatorial view, heteroaperturate, alternating colpori and pseudocolpi (**A**), polar view, polar area with triangular tenuitas (**B**)

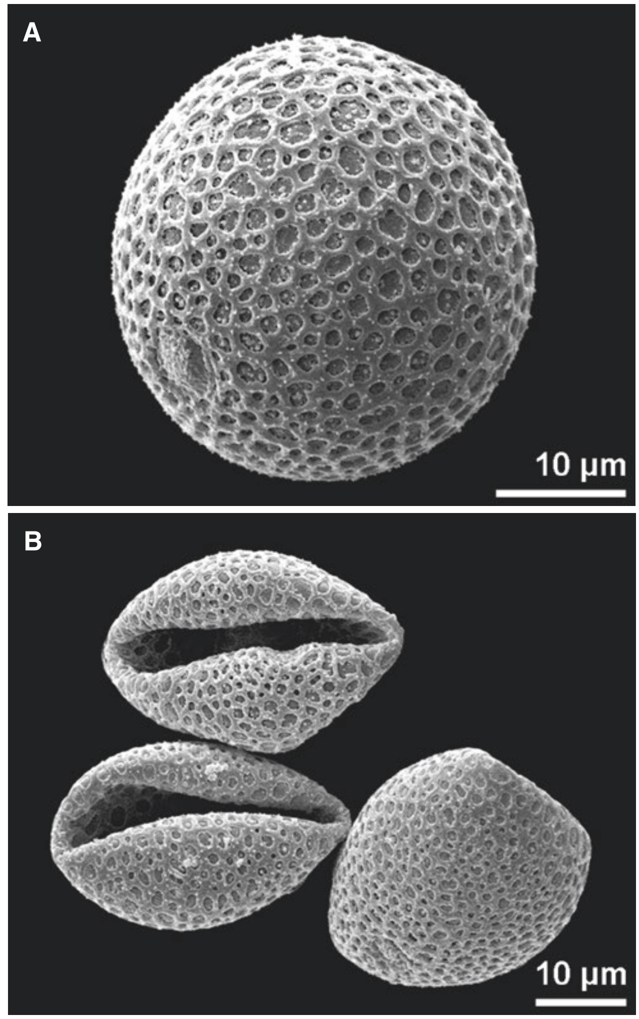

Fig. 14 Apertures in *Sparganium*. **A-B.** *Sparganium erectum*, Sparganiaceae, ulcerate, equatorial view hydrated pollen (**A**), boat-shaped, dry pollen (**B**)

Example 20: Preparation Effect — Areolate-Fossulate vs. Verrucate

The dehydration process with 2,2-dimethoxy-propane (DMP) and critical point drying (CPD) for SEM investigations can affect the ornamentation. An example for different interpretations in relation to a varying degree of hydration is *Trichosanthes anguina* (Cucurbitaceae), where the ornamentation can reflect different degrees of hydration. The ornamentation can be described as areolate and fossulate in partially hydrated condition or verrucate and perforate in fully hydrated condition (Fig. 20).

Example 21: Preparation Effect — Striate vs. Striato-reticulate

The ornamentation of *Amorphophallus longituberosus* pollen in dry condition or hydrated in water is striate, but after critical point drying it becomes striate to reticulate. The striate to reticulate ornamentation of *Amorphophallus longituberosus* is a result of an expanding thin surface layer (Fig. 21 D). During rehydration, the expansion of the thin layer itself forms a reticulum (Fig. 21 C), which finally ruptures partly or completely (Ulrich et al. 2017).

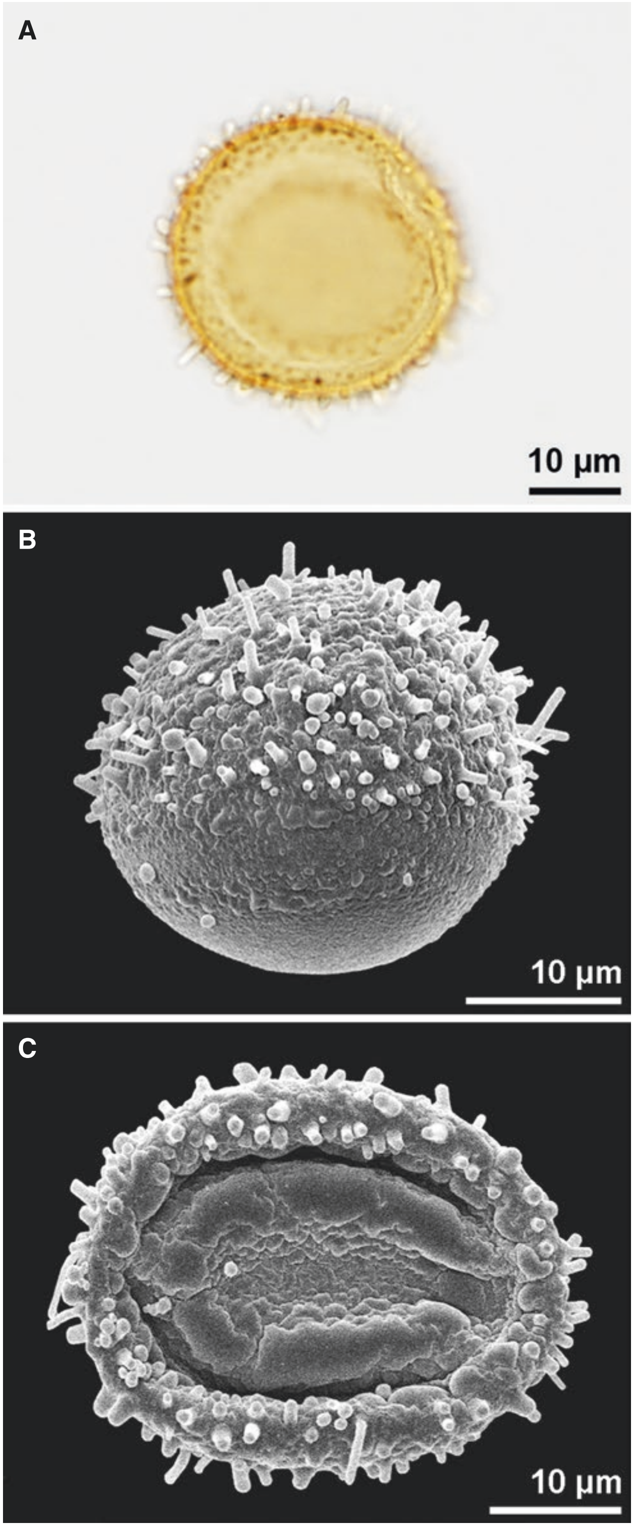

Fig. 15 Apertures in Nymphaea. **A-C.** *Nymphaea* sp., Nymphaeaceae; ring-like aperture, polar view (**A**), Ring-like aperture, equatorial view (**B**), dry pollen, cup-shaped (**C**)

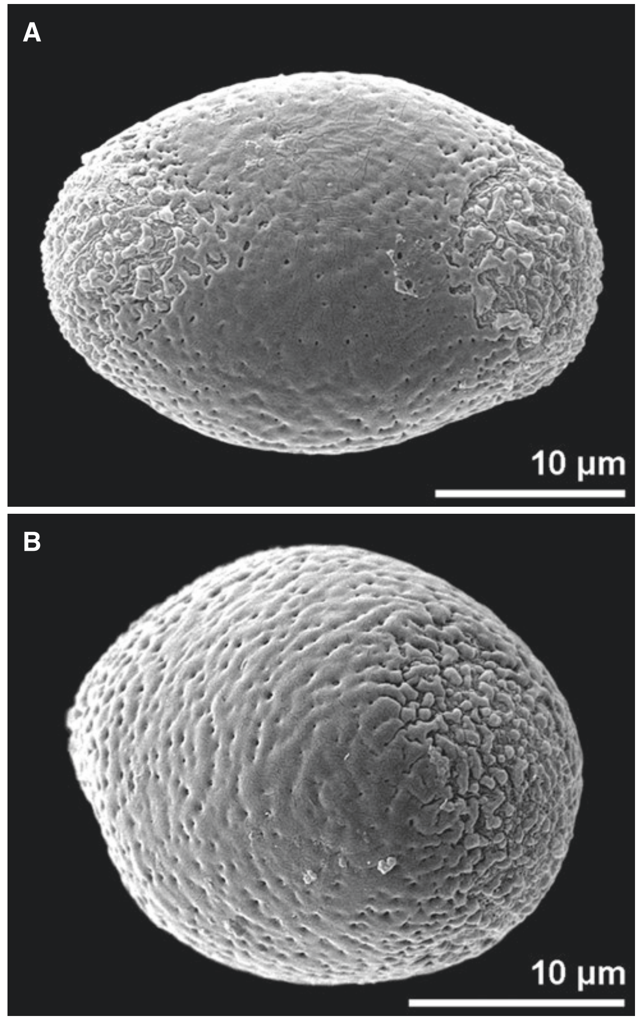

Fig. 16 Disulcate. **A-B.** *Calla palustris*, Araceae, polar and equatorial view

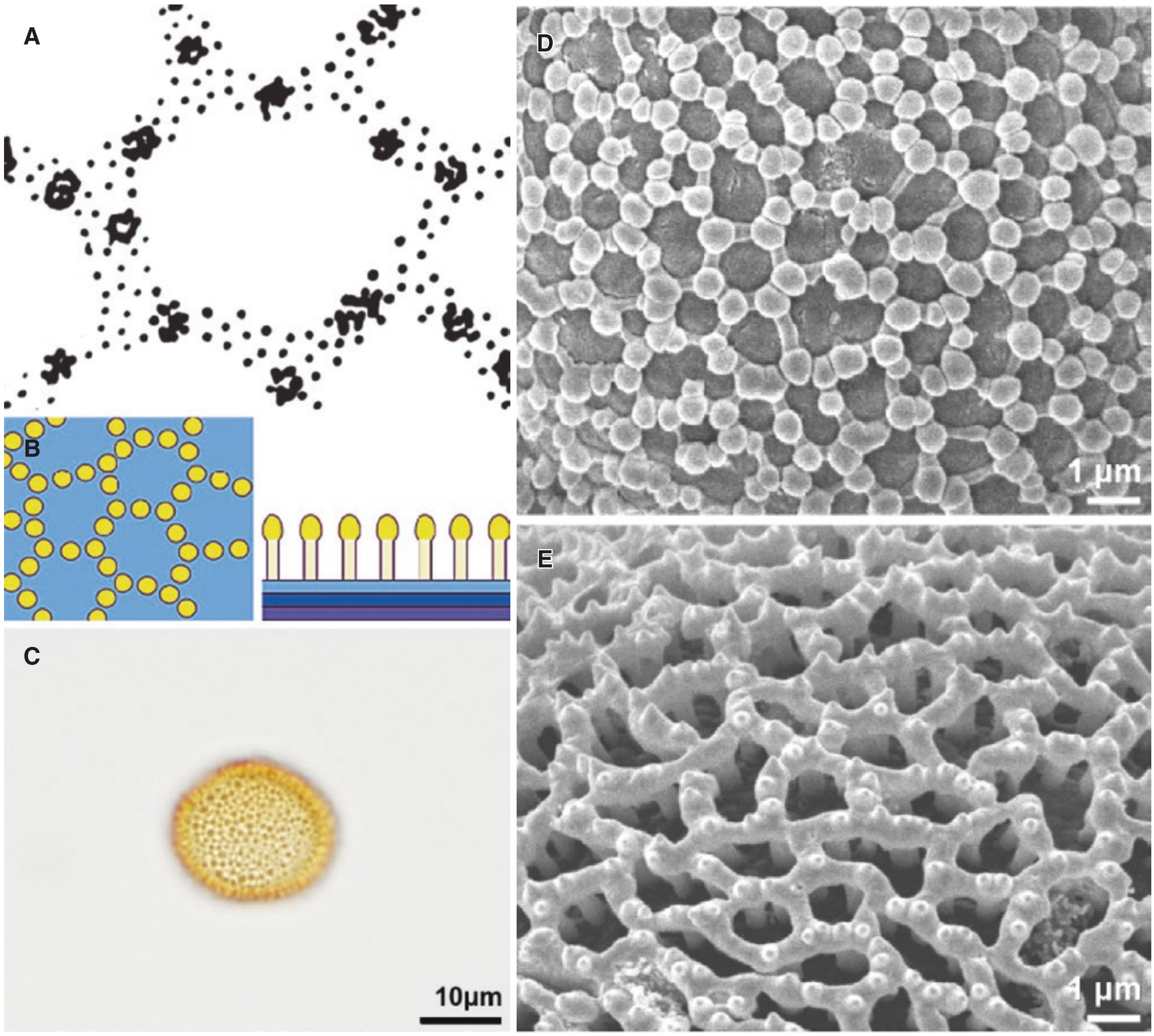

Fig. 17 Retipilate vs. reticulum cristatum. **A.** Drawing from Erdtman (1952). **B.** Drawings from Punt et al. (2007). **C.** *Callitriche palustris*, Plantaginaceae, acetolyzed pollen in LM. **D.** *Callitriche polymorpha*, Plantaginaceae, reticulum cristatum with small gemmae (suprasculpture) on thin muri. **E.** *Cuscuta lupuliformis*, Convolvulaceae, reticulum cristatum with nanoechini (suprasculpture)

Example 22: Staining Methods — Absence or Presence of Endexine

The staining behavior of the endexine is very heterogeneous, even within the same plant family or the same genus (Weber and Ulrich 2010). Therefore, the endexine is often reported as absent even though the layer is actually present. In most studies on pollen ultrastructure, sections are stained with uranyl acetate and lead citrate only. To truly distinguish the presence of endexine one should/must apply potassium permanganate which stains the endexine electron dense (Fig. 22, see also "Methods in Palynology").

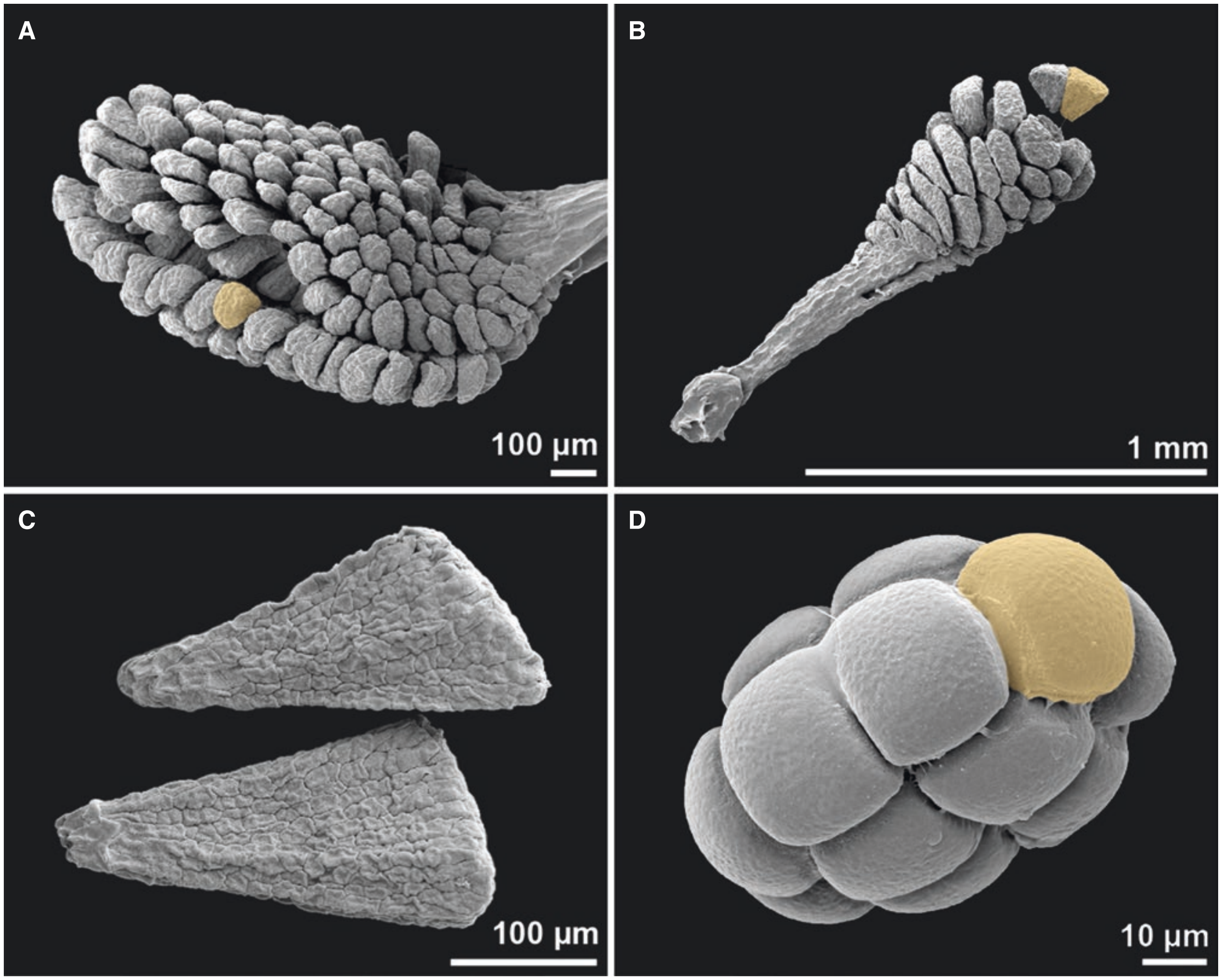

Fig. 18 Massula vs. polyad. **A.** *Habenaria* sp., Orchidaceae, pollinium composed of numerous massulae (massula highlighted). **B.** *Orchis ustulata*, Orchidaceae, pollinium composed of numerous massulae, two massulae partly segregated (massula highlighted). **C.** *Ludisia discolor*, Orchidaceae, 2 segregated massulae. **D.** *Albizia julibrissin*, Fabaceae, polyad (monad highlighted)

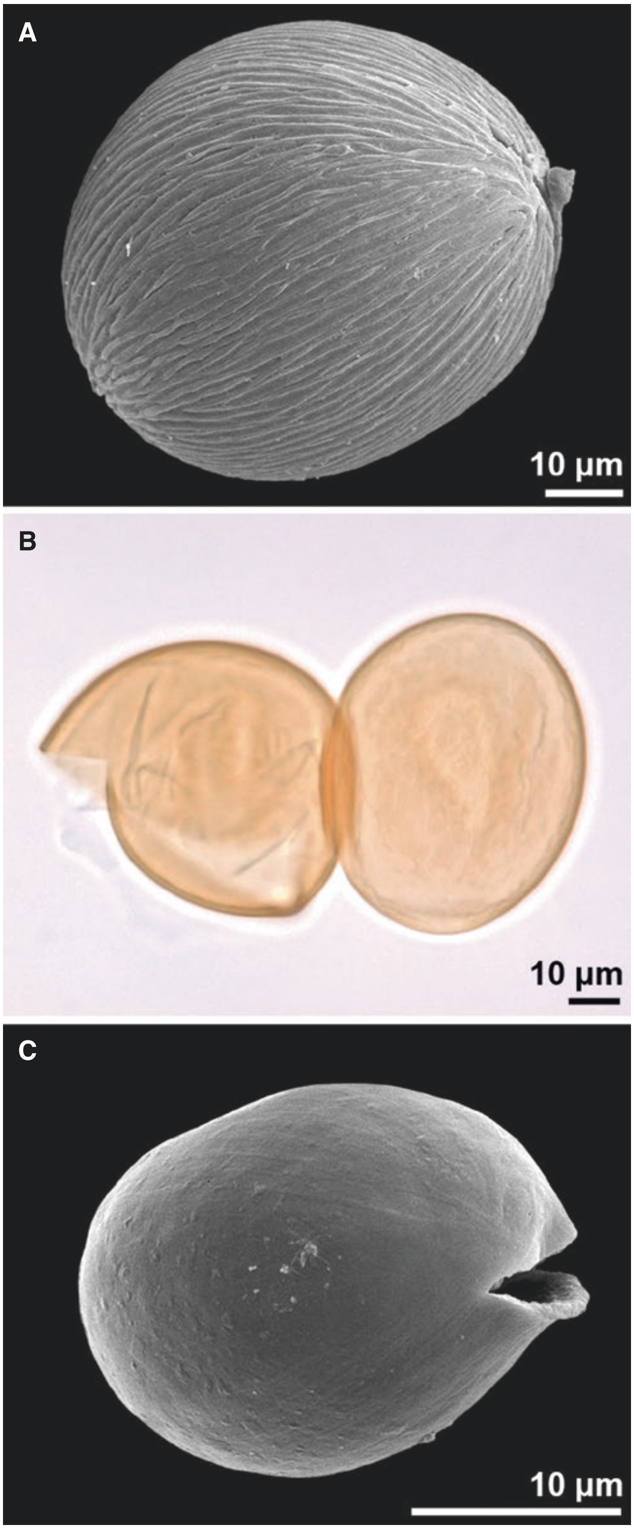

Fig. 19 Preparation effect — psilate vs. ornamented. A-C. *Amorphophallus krausei*, Araceae, pollen striate in hydrated condition (**A**), psilate after acetolysis, LM (**B**) and SEM (**C**)

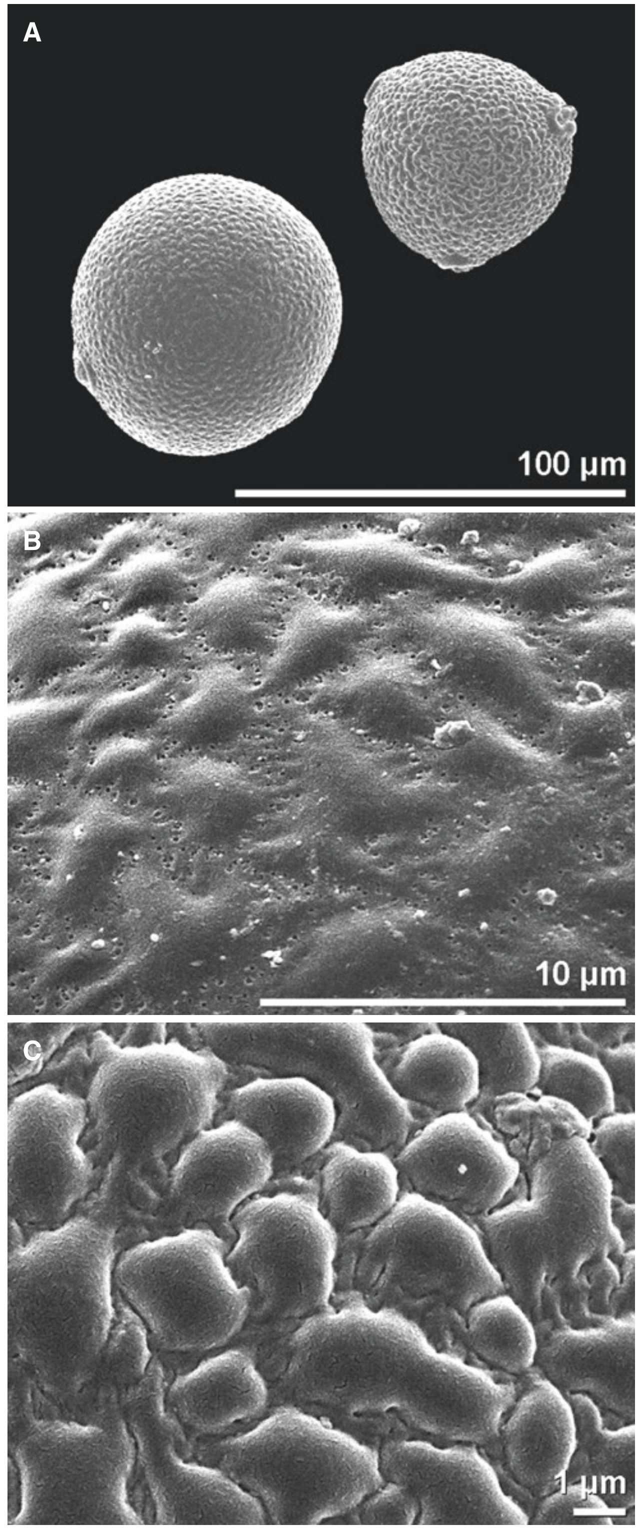

Fig. 20 Preparation effect on ornamentation. A-C. *Trichosanthes anguina*, Cucurbitaceae. **A.** Pollen at different state of hydration: fully hydrated (left), less hydrated (right). **B.** Hydrated pollen, surface detail, verrucate, perforate. **C.** Less hydrated, surface detail, areolate-fossulate

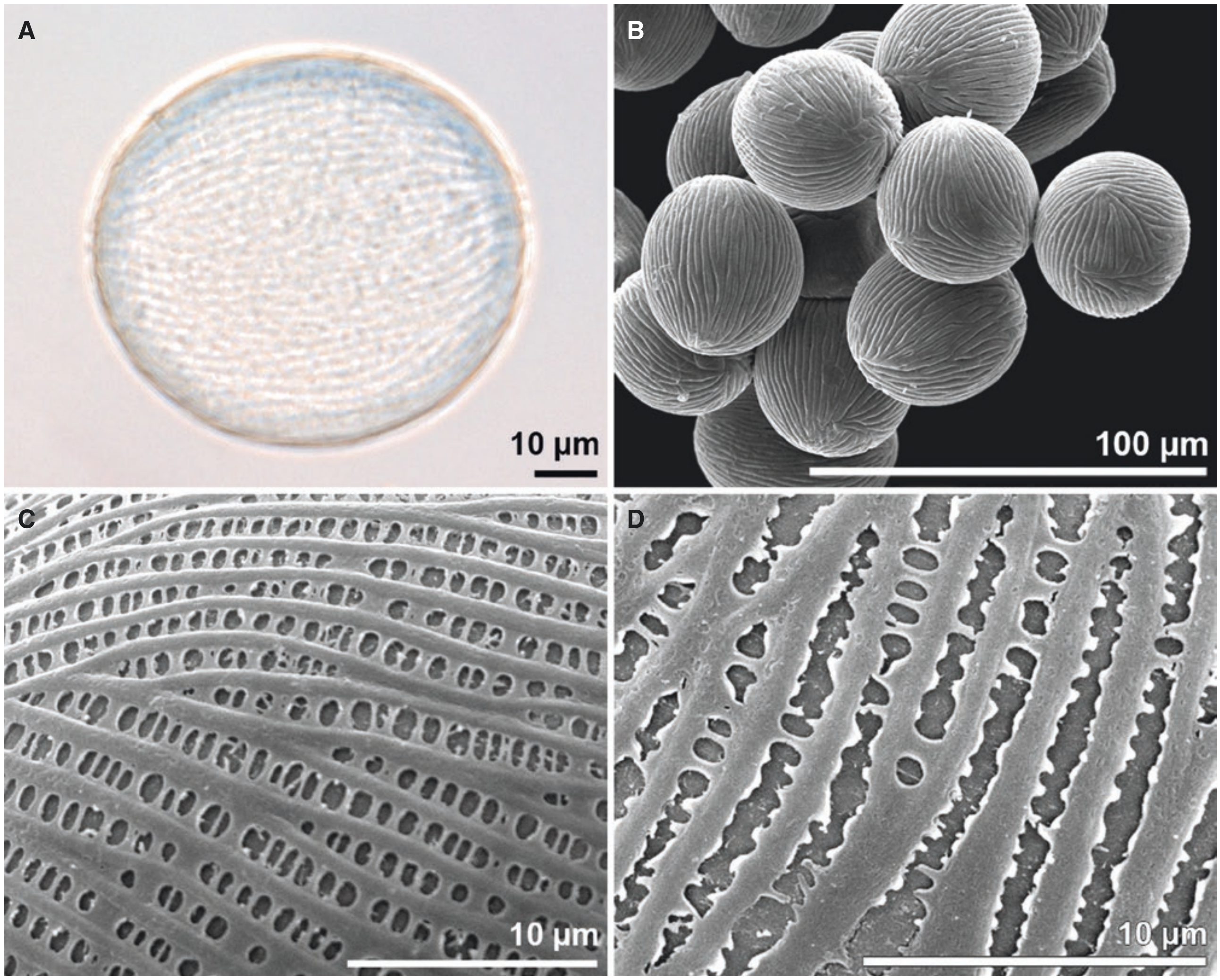

Fig. 21 Preparation effect on ornamentation. **A-D.** *Amorphophallus longituberosus*, Araceae, hydrated pollen in water with striate ornamentation, LM (**A**), dry pollen in SEM, striate (**B**), hydrated pollen in SEM, striate to reticulate (**C**), hydrated pollen in SEM, ornamentation striate with expanding thin surface layer (**D**)

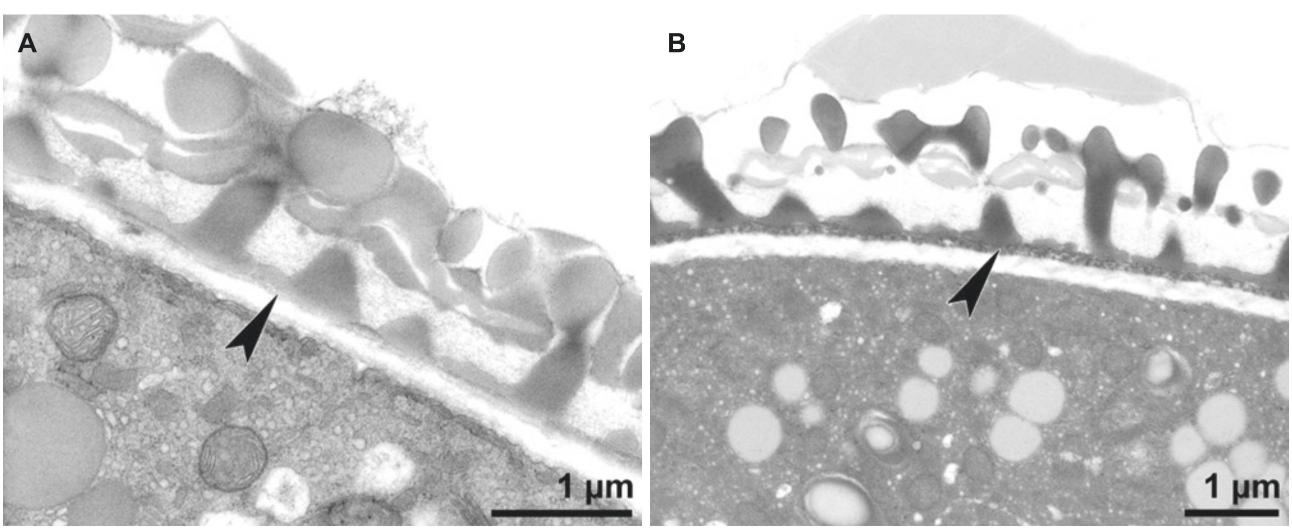

Fig. 22 Absence or presence of endexine. **A-B.** *Thymus odoratissimus*, Lamiaceae, U + Pb staining, endexine (arrowhead) not clearly visible (**A**), potassium permanganate staining, endexine (arrowhead) clearly visible (**B**)

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