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„Comparative pollen morphology of selected angiosperm species“

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Abstract

The pollen morphological characters of 17 selected angiosperm species were investigated to expand two databases – PalDat and eFlower – with new palynological information. The material was collected in the Botanical Garden of the University of Vienna (HBV), the Austrian Federal Gardens Schönbrunn and Belvedere. The pollen morphology was investigated by scanning electron microscopy. The present study demonstrates that pollen morphological studies are important in understanding evolutionary processes, in plant systematics, and in resolving taxonomic problems at family, generic, or species level.

The results show that monocot pollen is either sulcate or inaperturate, whereas the aperture condition in eudicot pollen is more diverse, ranging from three to more than six apertures. In the present study, differences and similarities between the selected species are illustrated and discussed.

Kurzfassung

Pollenmorphologische Merkmale von 17 ausgewählten Angiospermenarten wurden untersucht, um zwei Datenbanken – PalDat und eFlower – mit neuen palynologischen Informationen zu erweitern. Das Material wurde im Botanischen Garten der Universität Wien (HBV), den Österreichischen Bundesgärten Schönbrunn und Belvedere gesammelt. Die Pollenmorphologie wurde mittels Rasterelektronenmikroskopie untersucht. Die vorliegende Studie zeigt, dass pollenmorphologische Untersuchungen wichtig für das Verständnis evolutionärer Prozesse, die Systematik und die Lösung taxonomischer Probleme auf Familien-, Gattungs- oder Artebene sind.

Die Ergebnisse zeigen, dass Pollen inkeimblättriger Pflanzen (Monokotyledonen) entweder sulcat oder inaperturat sind, während die Keimöffnungen des Pollens zweikeimblättriger Pflanzen vielfältiger sind, und von drei bis mehr als sechs Aperturen reichen. In der vorliegenden Studie werden Unterschiede und Gemeinsamkeiten zwischen den ausgewählten Arten aufgezeigt und diskutiert.

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Introduction

Palynology is a scientific discipline concerned with the study of pollen, spores, and other microscopic entities, summarized as palynomorphs (Halbritter et al., 2018; Horčinová Sedláčková et al., 2020). Pollen represents the male gametophyte of seed plants, which produces the male gametes (sperm cells) (Stephen, 2014; Halbritter et al., 2018). During pollen dispersal and transport from the stamens to the pistil of angiosperms, the genetic material is protected by a highly resistant pollen wall (sporoderm). Pollen is morphologically diverse in e.g., size, surface ornamentation, aperture type and number, and shape (Stephen, 2014; Prieu et al.,2017; Halbritter et al., 2018).

Pollen is produced within the anthers, immersed in a locular fluid (Firon et al., 2012). When pollen is mature, the locular fluid disappears, and the anther opens releasing the pollen grains. Pollen is dispersed with variable water content, described as dry, partly dehydrated (semi-hydrated), or fully hydrated (Pacini et al., 2006). During pollen dispersal, pollen can be exposed to the environment for different periods and may rehydrate or dehydrate with changing environmental relative humidity, also affecting the viability of pollen over time (Nepi et al., 2001; Franchi et al., 2011; Firon et al., 2012). The ability of pollen to absorb and release water is described as harmomegathy (Halbritter et al., 2018). Harmomegathic mechanisms involve different pollen characters and infolding patterns are influenced by e.g., the pollen wall (thickening and thinning of wall components), aperture number and type, pollen size, ornamentation type, and presence of pollen coatings. According to the literature, it is impossible to predict the shape of pollen in dry conditions (Nepi et al., 2001; Halbritter & Hesse, 2004; Volkova et al., 2013; Doyle, 2015; Halbritter et al., 2018). Numerous pollen studies proved that different pollen grains sharing the same number and type of apertures may infold quite differently (e.g., Halbritter & Hesse, 2004; Halbritter et al., 2018; Božič & Šiber, 2020). The shape, P/E-Ratio, and size of pollen in hydrated as well as in dry conditions may vary and must therefore be described for both conditions.

Pollination

Pollen can be transferred through biotic and abiotic vectors (Nguyen & Weber, 2015). The pollen transport of an estimated 12,5% of angiosperms species occurs by wind (anemophily) or water (hydrophily) (Ollerton et al., 2011). In both cases, stigmas and anthers must be exposed, and pollen grains must be produced in large quantities (Ackerman, 2000). Pollen of the remainder of angiosperm species (ca. 87,5%) is transported through biotic vectors, which include animals such as insects, mammals, birds, etc. (Ollerton et al., 2011). Animal pollination (zoophily) plays a crucial role in pollen

transfer in angiosperms and has also been shown to be ancestral in this group of plants (Friis et al., 2011). Pollinators are attracted by the color, scent, and shape of flowers. Pollen must be attached to their body and transferred to other flowers (Schiestl & Johnson, 2013). Pollen can also be presented to pollinators on other floral organs, such as petals or styles. This type is called secondary pollen presentation (Endress, 1996).

Phylogeny and evolution of angiosperms

Angiosperms are present in almost all terrestrial and aquatic ecosystems today. The fossil record suggests that angiosperms first diversified between the Barremian and Albian of the Early Cretaceous (Coiro et al., 2019). Angiosperm flowers from this time period are very small. Since the Late Cretaceous, angiosperms have been the dominant plant group on Earth with more than 350,000 extant species (Friis et al., 2011). The differentiating morphological and ultrastructural features observed in extant pollen are the direct results of their varied evolutionary pathways taken place over the last c. 130 million years. Pollen morphology of extant plants, in combination with a proper phylogenetic framework, is therefore vital to trace back the evolutionary steps in pollen development and evolution. According to Walker and Doyle (1975), angiosperm pollen can be divided into two types: 1) sulcate and sulcate-derived, and 2) tricolpate and tricolpate-derived.

Sulcate pollen is the ancestral form found in early diverging angiosperms (ANA grade), magnoliids, and monocots. Pollen of this type is equipped with a single aperture and shows a reticulate sculpture. Several authors (e.g., Couper, 1958; Doyle, 2005) assigned such fossil pollen grains to *Clavatipollenites* and affiliated it with the family Chloranthaceae, but similar pollen is also found in Myristicaceae, Canellaceae, Aristolochiaceae, and Austrobaileyaceae. Sulcate pollen later evolved into tricolpate or triporate pollen (and pollen with more than three apertures) (Walker & Doyle, 1975).

Tricolpate and derived pollen types appear for the first time in the Albian fossil record and have been described from Early Cretaceous sediments from South America, Africa, and the Middle East. Tricolpate aperture arrangement is a synapomorphy for the eudicot clade, which comprises ca. 75% of all extant angiosperm including the two major lineages Rosidae and Asteridae. In the Late Cretaceous triporate pollen (with three round apertures) referred to the Normapolles group evolved (Doyle, 2005, 2012, 2015; Friis et al., 2011).

Evolution of pollen characters

An important character to elucidate the phylogeny of angiosperms is the **pollen wall.** The pollen wall is, from a structural point of view, very diverse. In the majority of angiosperms, the pollen wall consists of two layers: the inner intine and the outer exine. Exceptions are present within aquatic angiosperms, where the pollen wall is extremely reduced and lacks an exine (Walker & Doyle, 1975). One of the main substances of the exine is sporopollenin, a highly resistant biopolymer, which makes the pollen wall extremely resistant, and therefore can be preserved in sedimentary rocks (Halbritter et al., 2018).

A pollen unit is a group of mature pollen grains located inside the anther locules of the stamen (Walker & Doyle, 1975). Pollen of most early diverging angiosperms is dispersed as monads (a single pollen grain). Dyads (two pollen grains in one unit) evolved from monads and occur mostly in the two families Podostemaceae and Scheuchzeriaceae (Walker & Doyle, 1975). Tetrads (four pollen grains in one unit) developed separately in many groups, such as Juncaceae, Thurniaceae, and Typhaceae (Walker & Doyle, 1975; Halbritter et al., 2018). Pseudomonads (cryptotetrads) evolved from tetrads and are presently found only in Cyperaceae. It is assumed that polyads emerged from tetrads or monads. Massulae and pollinia are the most complex pollen units and are present only in two families - Apocynaceae and Orchidaceae (Walker & Doyle, 1975).

Pollen size is taxon dependent but can be affected by preparation methods and the degree of hydration. The size of pollen of taxa is an important character that must be considered while determining any particular taxon. However, it can never be taken as a single determination factor and must always be brought in correlation with other characters of the pollen. The pollen size in angiosperms ranges from 2 to 5 µm in *Myosotis* (Boraginaceae) to rarely more than 300 µm in some Annonaceae and some monocots. According to Walker and Doyle (1975), one of the largest pollen grains in angiosperms is found in *Cymbopetalum odoratissium* with a size of 350 µm and pollen grains of some marine angiosperms, e.g., *Zostera* (Zosteraceae) and *Cymodocea* (Zannichelliaceae), may be more than 2000 µm in diameter.

Pollen shape mostly depends on the type of aperture, polarity and symmetry. Sulcate grains are usually boat-shaped, heteropolar, and bilateral. Colpate grains are generally spheroidal and isopolar. Inaperturate pollen is usually spheroidal and apolar. Boat-shaped pollen is considered to represent an ancestral stage and spheroidal pollen a derived character-state at the level of angiosperms. Spheroidal inaperturate pollen appears to

have developed from boat-shaped sulcate pollen and may have developed into either oblate or prolate pollen (Walker & Doyle, 1975).

The aperture type is a very important systematic character, together with the pollen wall. The ancestral aperture type is a sulcus that evolved at the distal pole. Two basic aperture types have been identified in angiosperms: 1) a sulcus located at the distal pole, and 2) three colpi situated at the equator. Sulcate pollen occurs in gymnosperms, early diverging angiosperm lineages, and monocots, while colpate pollen is restricted to eudicots (Walker & Doyle, 1975; Halbritter et al., 2018).

Pollen polarity is determined by the aperture condition and shape (Walker & Doyle, 1975; Halbritter et al., 2018). Sulcate pollen is heteropolar. From heteropolar pollen, isopolar inaperturate pollen developed, and then further basic isopolar colpate pollen of eudicots has evolved. From isopolar colpate pollen, isopolar inaperturate, rugate and porate (synonym: forate) pollen, as present in some eudicots, has been derived secondarily (Walker & Doyle, 1975).

Pollen symmetry is determined by the shape, particularly the number of vertical planes and length of the equatorial axis, and the aperture arrangement. Bilateral symmetry is present in boat-shaped sulcate pollen. Later, the radial symmetry of the eudicot pollen developed. This kind of symmetry evolved also in biradial pollen (e.g., dicolpate, diporate, disulculate pollen). An important character of these types of grains is the presence of two apertures and the shape, that changes from spherical to equatorially elongated. The result of this change is the evolution of secondarily bilateral pollen (Walker & Doyle, 1975).

The role of pollen in systematics

Pollen features may be useful in various scientific disciplines, such as ecology, melissopalynology, paleobotany, aeropalynology, criminology (e.g., Santra et al., 1991; Mildenhall et al., 2006; Stephen, 2014; Fernandes Pinto da Luz et al., 2018; Salamma et al., 2019). Descriptive pollen characters include the size, shape, surface ornamentation, number and type of apertures, symmetry, and polarity. Some of these features are important for systematics, reflecting phylogenetic relationships. Moreover, they are useful for delimitation of taxa, for solving interrelationships between various taxa, including their classification on the level of families, subfamilies, tribes, genera, or even species (Ragho, 2020). Pollen characters such as aperture number, shape and ornamentation, are crucial features for the determination of pollen types. For example, the type of ornamentation may have systematic significance in the determination of tribes or species within a genus

(Ferguson, 1985; Wronska-Pilarek & Jagodzinski, 2011; Aguilar-García et al., 2012; Ibrahim Gabr, 2018; Ragho, 2020).

eFLOWER and PalDat database

The present thesis is associated with two scientific projects, eFLOWER initiative and PalDat database. The aim is to contribute to the expansion of these two databases with the results from the present study.

The eFLOWER project aims to answer questions about the evolution and diversification of angiosperms, e.g. “What were flowers like in deep nodes of the angiosperm tree? Which floral innovations are linked with major increases in diversification rates? How are floral characters correlated with one another? To what extent has floral diversification been driven by pollination? Where do fossil flowers fit on the phylogeny of extant angiosperms?”, and many more (http://eflower.myspecies.info/). To answer all these questions, numerous floral characters must be collected and scored for different angiosperm taxa. These characters are included in the associated database “PROTEUS”, which forms the core of the eFLOWER project (Sauquet, 2019). It represents the largest dataset of floral morphological traits of angiosperm species ever assembled, including pollen characters. The present study contributes data to different research projects, and at the same time, extend the database of eFLOWER with new informations. For example, samples from „792 species, 63 orders (98 %) and 372 families (86 %) of angiosperms were used, from the PROTEUS database, for the reconstruction of the first model of ancestral flowers at the deepest nodes in the phylogeny of angiosperms“ (Sauquet et al., 2017). Their results showed that the ancestral flower „was most likely bisexual and had an undifferentiated perianth of more than ten tepals, an androecium of more than ten stamens, and a gynoecium of more than five carpels. Perianth and androecium probably had whorled phyllotaxis with three organs per whorl“ (Sauquet et al., 2017). The combination of characters present in the first ancestral flower is unique, and „there is no living species that shares this exact combination of characters“, only similarities (Sauquet et al., 2017). The eFLOWER database proved to be a useful tool for botanical studies and contributes to a better understanding of phylogenetic relationships in angiosperms (Sauquet et al.,2017; Schönenberger et al., 2020).

The database **PalDat** is a palynological database, maintained by members of the pollen group at the Division of Structural and Functional Botany at the University of Vienna (PalDat, 2000 onwards). The database includes datasets with pollen descriptions and images of angiosperm and gymnosperm pollen. The datasets include light microscopic

(LM), scanning electron microscopic (SEM) and transmission electron microscopic (TEM) images. At present PalDat contains more than 35,000 pictures from 4,434 plant species and it is constantly updated with new species. The main idea of PalDat „is to increase the amount of data in the database by offering a tool for global online submission and publication“ (Weber & Ulrich, 2017). It is possible to publish palynological data as an author or to contribute as a co-author to an existing publication (PalDat, 2000 onwards; Weber & Ulrich, 2017). Moreover, online access to the database is free, and the data are available to everyone who is interested in pollen.

For the present pollen morphological study, the material was investigated by scanning electron microscopy (SEM). The most important pollen characteristics (shape, size, symmetry, polarity, aperture type and ornamentation type) have been researched to describe and distinguish pollen of the studied species. Systematic aspects and morphology were the topics, that have been studied in the present master thesis. The results will be submitted to the PROTEUS database and the pollen database PalDat.

Material and Methods

Investigated species

For the present thesis, the pollen morphology of 17 species was investigated by scanning electron microscopy. Fresh flowers and herbarium vouchers were collected from the Botanical Garden of the University of Vienna (HBV), the Austrian Federal Gardens Schönbrunn and Belvedere (Table 1, Fig. 1A). The samples were air-dried and stored in small paper bags from July 2019 till September 2020. Vouchers of the investigated taxa were deposited in the herbarium of the University of Vienna (WU), except for *Iris missouriensis, Jacaranda mimosifolia, Spathiphyllum wallisii, Heuchera micrantha* and *Dalechampia spathulata.* From these species only a few flowers were available, and all the material was used for pollen analysis.

Scanning Electron Microscopy

The preparation method of pollen in hydrated and dry conditions followed the DMP direct method of Halbritter (1998). According to Halbritter (1998), this method preserves the morphologically important features of pollen grains like e.g., size, shape, and surface details. All samples were investigated using a Jeol - JSM-6390 scanning electron microscope (Fig. 2F).

Preparation of pollen grains in hydrated condition. —Anthers and/or dispersed pollen grains were prepared from fresh flowers or herbarium material under the dissecting microscope (Fig. 1B-C), transferred into small pouches made of filter paper, and labeled (Fig. 1D – E). The samples were hydrated in drops of tap water for about 10 seconds, dehydrated in acidified 2,2 dimethoxypropane (DMP) for 20 minutes (Fig. 1F), followed by pure acetone for 10 minutes. Critical point drying (CPD) was performed in a “Tousimis Supercritical Autosamdri-815”, using carbon dioxide (CO_2) and acetone as intermediate fluid (Fig. 2A). The critical point dried pollen samples were mounted on aluminum stubs, using double-sided adhesive tape, and sputter coated with gold using a Bal-Tec SCD 050 sample sputter coater (Fig. 2B-E).

Preparation of pollen grains in dry condition. —The air-dried samples were dehydrated in acidified 2,2-dimethoxypropane (DMP) and critical point dried. The samples were mounted on aluminum stubs, using double-sided adhesive tape and sputter coated with gold.

Figure 1: Preparation of samples for scanning electron microscopy (SEM)

A. Anthers/pollen collected from flowers at anthesis (example: *Pittosporum tobira*)

B-C. Preparation of pollen samples under the dissecting microscope

D. Pollen and parts of anthers transferred to a filter pouch

E. Ready-made and labeled filter pouches with fresh, or air-dried pollen samples inside

F. Dehydration of samples in acidified 2,2 dimethoxypropane

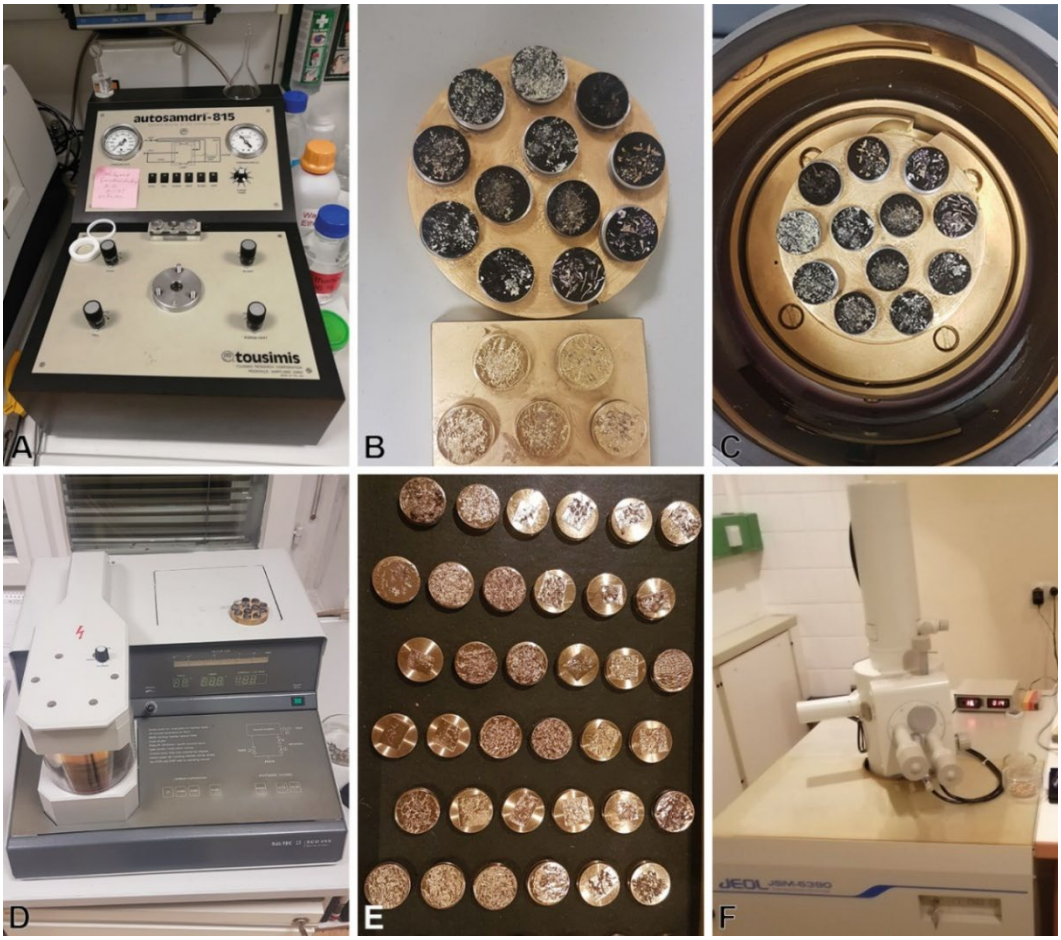

Figure 2: Preparation of samples for scanning electron microscopy (SEM)

A. Critical Point Dryer (Tousimis Supercritical Autosamdri-815)

B. Mounted samples on aluminum stubs

C. Samples placed inside the sputter coater chamber

D. Sputter coater (Bal-Tec SCD 050)

E. Ready-made gold coated samples

F. Scanning electron microscope (Jeol-JSM-6390)

Table 1: List of investigated species in alphabetical order, collected in the Botanical Garden of the University of Vienna (HBV) and the Austrian Federal Gardens Schönbrunn and Belvedere

Name of species[1]	Family	Accession number(s)	Location
Acorus calamus	Acoraceae	0005267	Schönbrunn (System 27 f)
Agapanthus africanus	Amaryllidaceae	0014293	HBV (Group 19 19170)
Albuca bracteata	Asparagaceae	0000751 0016108 0016109	Belvedere (A 192; A 183)
Aquilegia canadensis	Ranunculaceae	0000589	Belvedere (A 602)
Dalechampia spathulata	Euphorbiaceae	0014445	Schönbrunn
Geranium sanguineum	Geraniaceae	0001946	HBV (Group 13 13/03)
Heuchera micrantha	Saxifragaceae	0006355	Schönbrunn (System 18f)
Iris missouriensis	Iridaceae	0022490	HBV (Group 51 ALP C)
Jacaranda mimosifolia	Bignoniaceae	0011145	Schönbrunn (Reservegarten; Hibernation house)
Pellionia repens	Urticaceae	0015738 0020252 0020253	HBV (Hibernation house G18)
Perilla frutescens	Lamiaceae	0030103	HBV (Group 12)
Reseda alba	Resedaceae	0001960	HBV (Group 9; 09/06)
Rivina humilis	Petiveriaceae	0015199	HBV (Hibernation house G18)
Spathiphyllum wallisii	Araceae	0013891	HBV (Hibernation house)
Telephium imperati	Caryophyllaceae	0026724	HBV (Group 10; 10/06)
Tradescantia spathacea	Commelinaceae	0015454	HBV (G18)
Tribulus terrestris	Zygophyllaceae	0026928	HBV (Group 7 07/07)

[1]Color code: Orange – monocots; Blue – eudicots;

Results

In the present thesis, the pollen morphology of 17 angiosperm species (Table 2) was investigated in dry and hydrated conditions.

Table 2: Figure plates of investigated species, alphabetically sorted by order

Order	Family	Species [2]	Page numbers
Acorales	Acoraceae	*Acorus calamus*	12-14
Alismatales	Araceae	*Spathiphyllum wallisii*	15-17
Asparagales	Amaryllidaceae	*Agapanthus africanus*	18-20
Asparagales	Asparagaceae	*Albuca bracteata*	21-23
Asparagales	Iridaceae	*Iris missouriensis*	24-26
Brassicales	Resedaceae	*Reseda alba*	27-29
Caryophyllales	Petiveriaceae	*Rivina humilis*	30-32
Caryophyllales	Caryophyllaceae	*Telephium imperati*	33-35
Commelinales	Commelinaceae	*Tradescantia spathacea*	36-38
Geraniales	Geraniaceae	*Geranium sanguineum*	39-41
Lamiales	Bignoniaceae	*Jacaranda mimosifolia*	42-44
Lamiales	Lamiaceae	*Perilla frutescens*	45-46
Malpighiales	Euphorbiaceae	*Dalechampia spathulata*	47-49
Ranunculales	Ranunculaceae	*Aquilegia canadensis*	50-52
Rosales	Urticaceae	*Pellionia repens*	53-55
Saxifragales	Saxifragaceae	*Heuchera micrantha*	56-58
Zygophyllales	Zygophyllaceae	*Tribulus terrestris*	59-61

[2] Color code: Orange – monocots; Blue – eudicots;

Acorus calamus (Acorales, Acoraceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **small (10-25 µm)**	Shape (Dry Pollen): **cup-shaped**
Pollen Class: **sulcate**	Outline in Polar View (Dry Pollen): **elliptic**
Polarity: **heteropolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **1**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **sulcate**	Ornamentation SEM: **perforate, psilate**
Aperture Type: **sulcus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **present**	

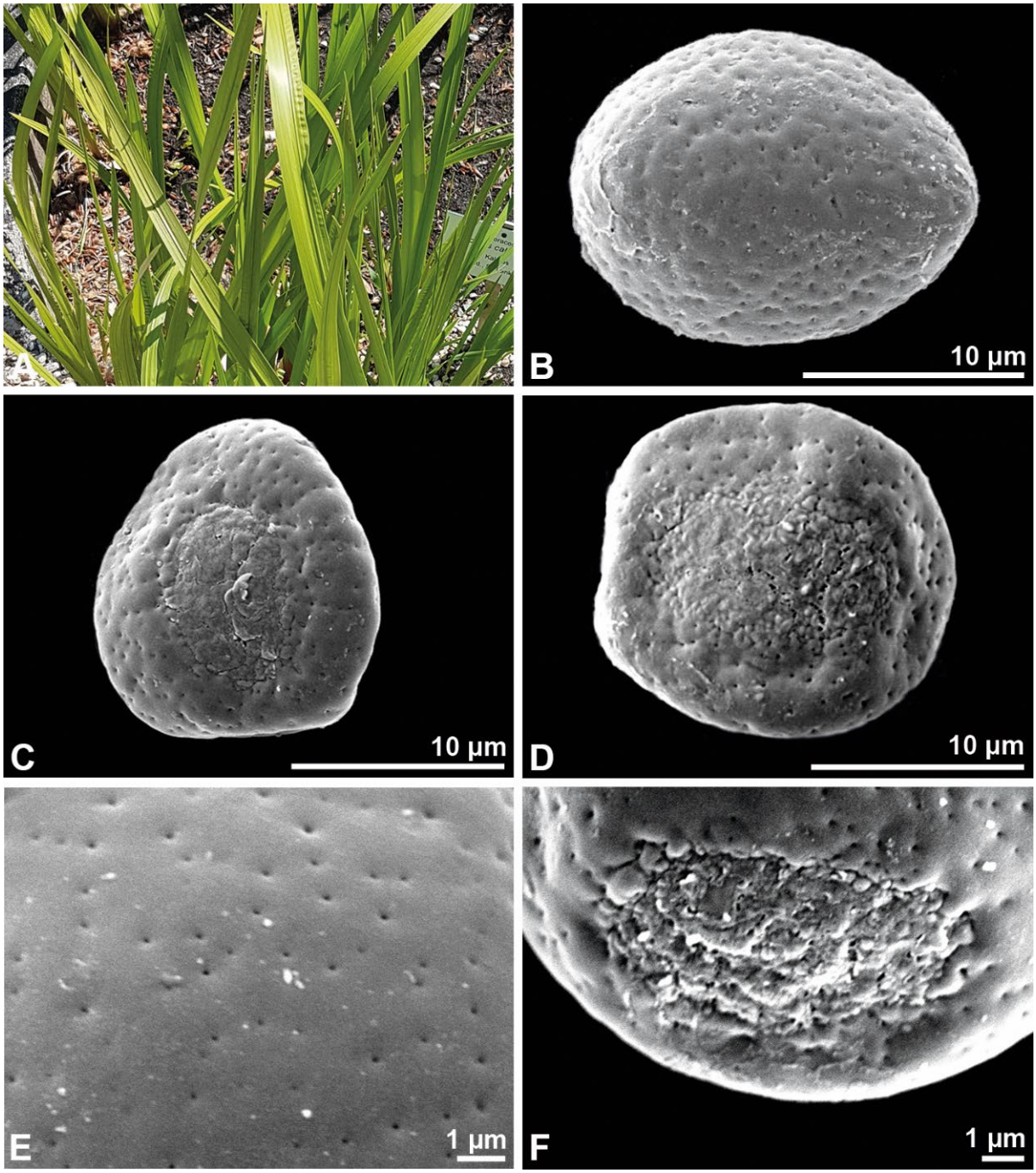

Figure 3: Plant image and scanning electron micrographs of *Acorus calamus* (DMP+CPD)

A. Habitus

B. Hydrated pollen grain in proximal polar view

C-D. Hydrated pollen grain in distal polar view

E. Detail of exine

F. Detail of aperture

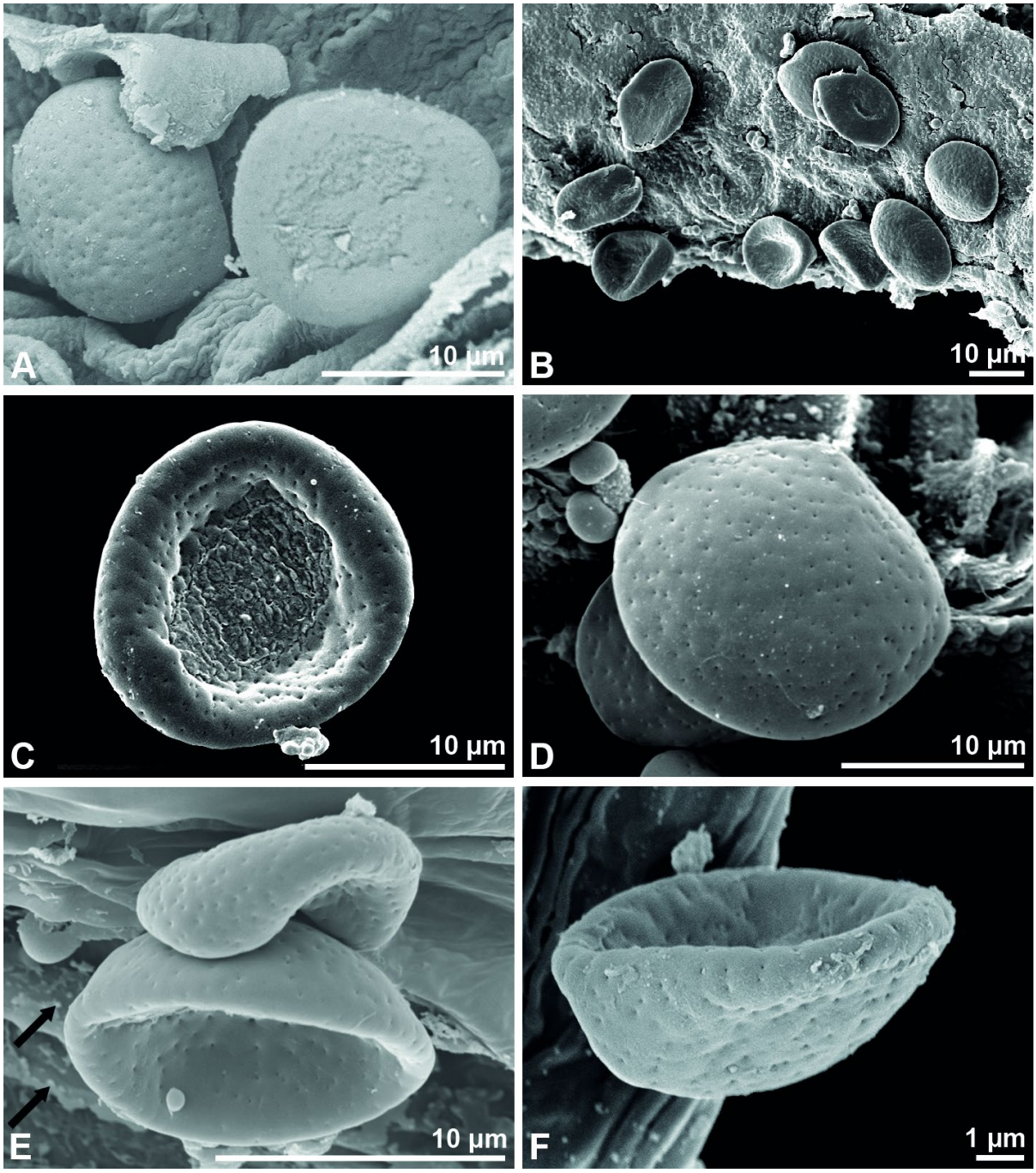

Figure 4: Scanning electron micrographs of *Acorus calamus* (DMP+CPD)

A. Hydrated pollen in polar proximal (left) and polar distal view (right)

B. Overview of dry pollen grains attached to the inner anther wall

C-D. Dry pollen grains cup-shaped; distal polar view (**C**) and proximal polar view (**D**)

E-F. Dry pollen cup-shaped; proximal view; Ubisch bodies attached to inner anther wall (arrows)

Spathiphyllum wallisii (Alismatales, Araceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal to elliptical**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **small (10-25 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **plicate**	Outline in Polar View (Dry Pollen): **elliptic**
Polarity: **isopolar**	Infoldings (Dry Pollen): **n/a**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **none**	Aperture Peculiarities: **n/a**
Aperture Condition: **inaperturate**	Ornamentation SEM: **plicate**
Aperture Type: **no aperture**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

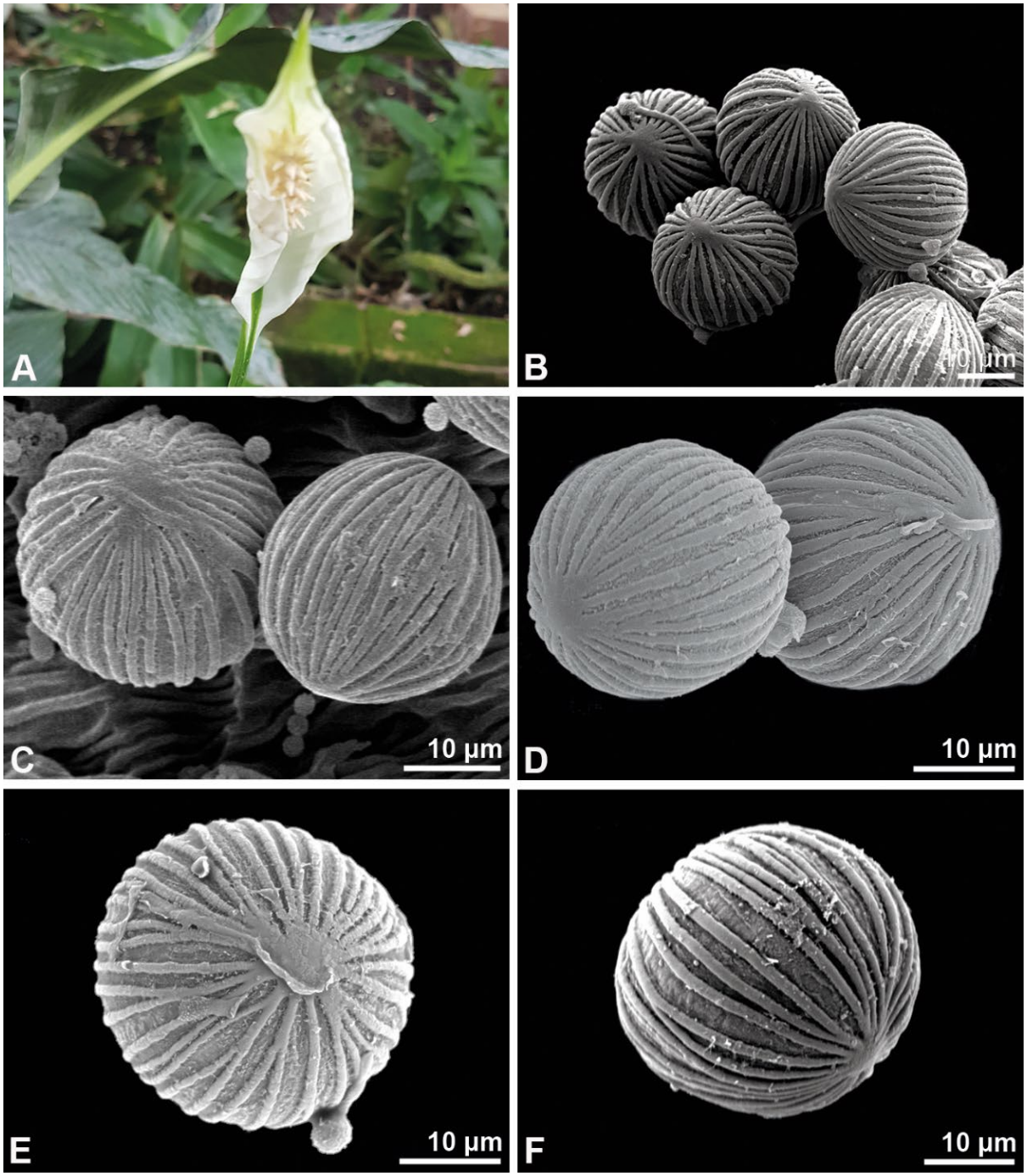

Figure 5: Plant image and scanning electron micrographs of *Spathiphyllum wallisii* (DMP+CPD)

A. Inflorescence

B-D. Hydrated pollen grains in the overview

E. Hydrated pollen grain in polar view, with a fungal spore attached to the pollen wall

F. Hydrated pollen grain in equatorial view

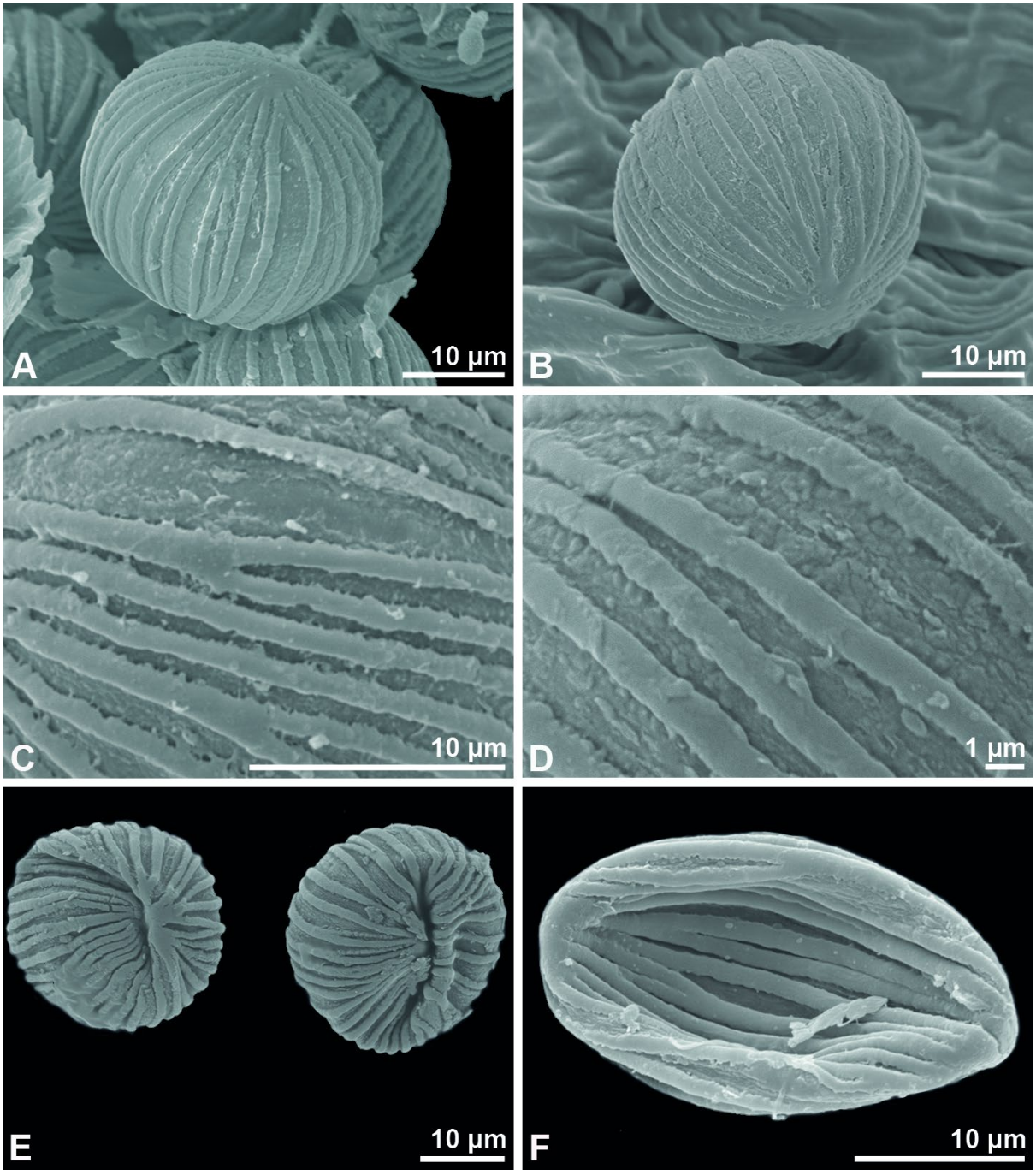

Figure 6: Scanning electron micrographs of *Spathiphyllum wallisii* (DMP+CPD)

A. Hydrated pollen in oblique view

B. Hydrated pollen attached to the inner anther wall

C-D. Exine surface

E-F. Dry pollen grains

Agapanthus africanus (Asparagales, Amaryllidaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **elliptical**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **medium-sized (26-50 µm)**	Shape (Dry Pollen): **boat-shaped**
Pollen Class: **sulcate**	Outline in Polar View (Dry Pollen): **elliptic**
Polarity: **heteropolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **1**	Aperture Peculiarities: **aperture membrane psilate**
Aperture Condition: **sulcate**	Ornamentation SEM: **microreticulate, heterobrochate**
Aperture Type: **sulcus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **present**	

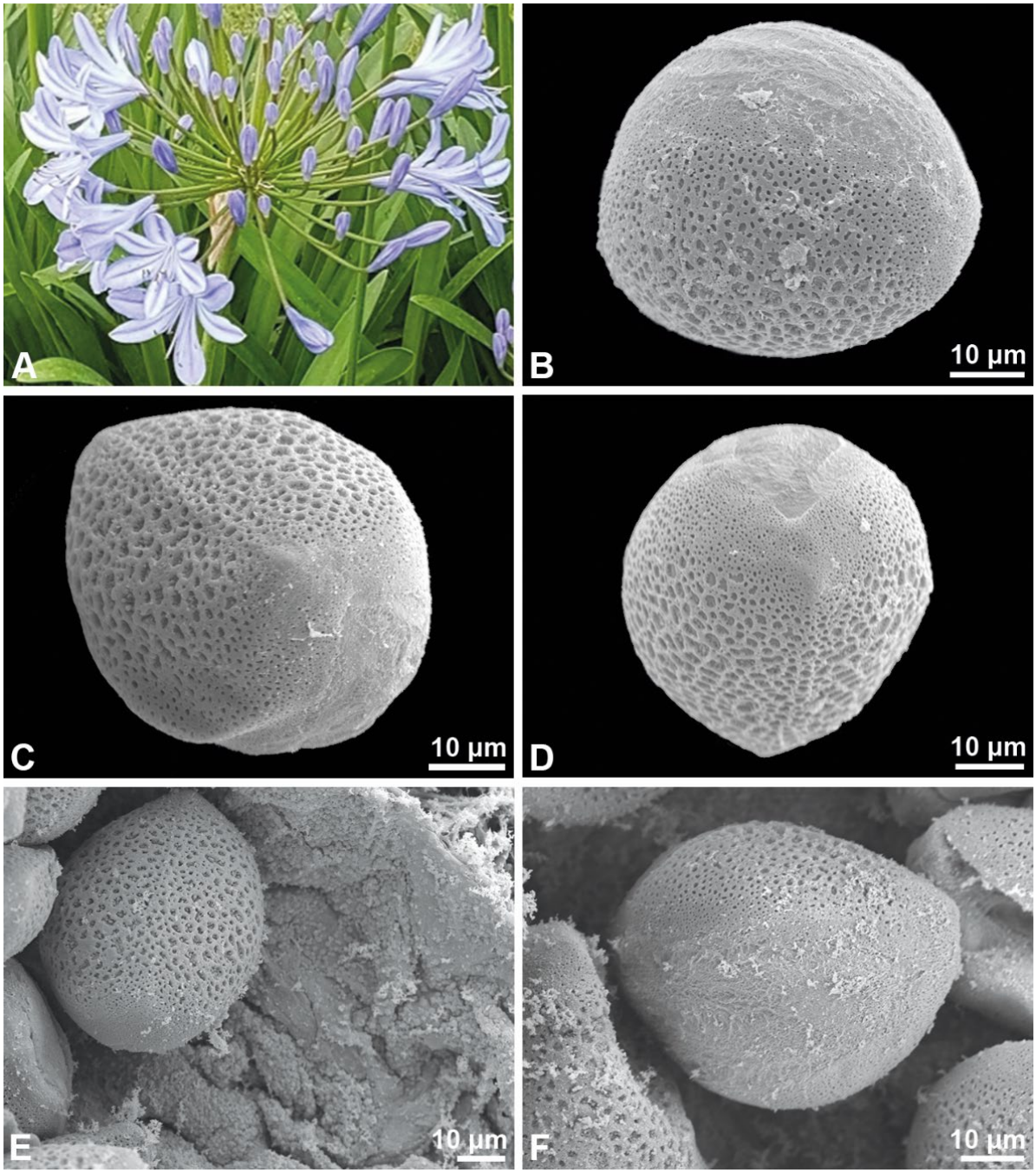

Figure 7: Plant image and scanning electron micrographs of *Agapanthus africanus* (DMP+CPD)

A. Inflorescence/flowers

B. Hydrated pollen grain in equatorial view (long axis)

C-D. Hydrated pollen grain in equatorial view (short axis)

E. Hydrated pollen in proximal polar view, attached to the inner anther; Ubisch bodies present

F. Hydrated pollen grain in distal polar view

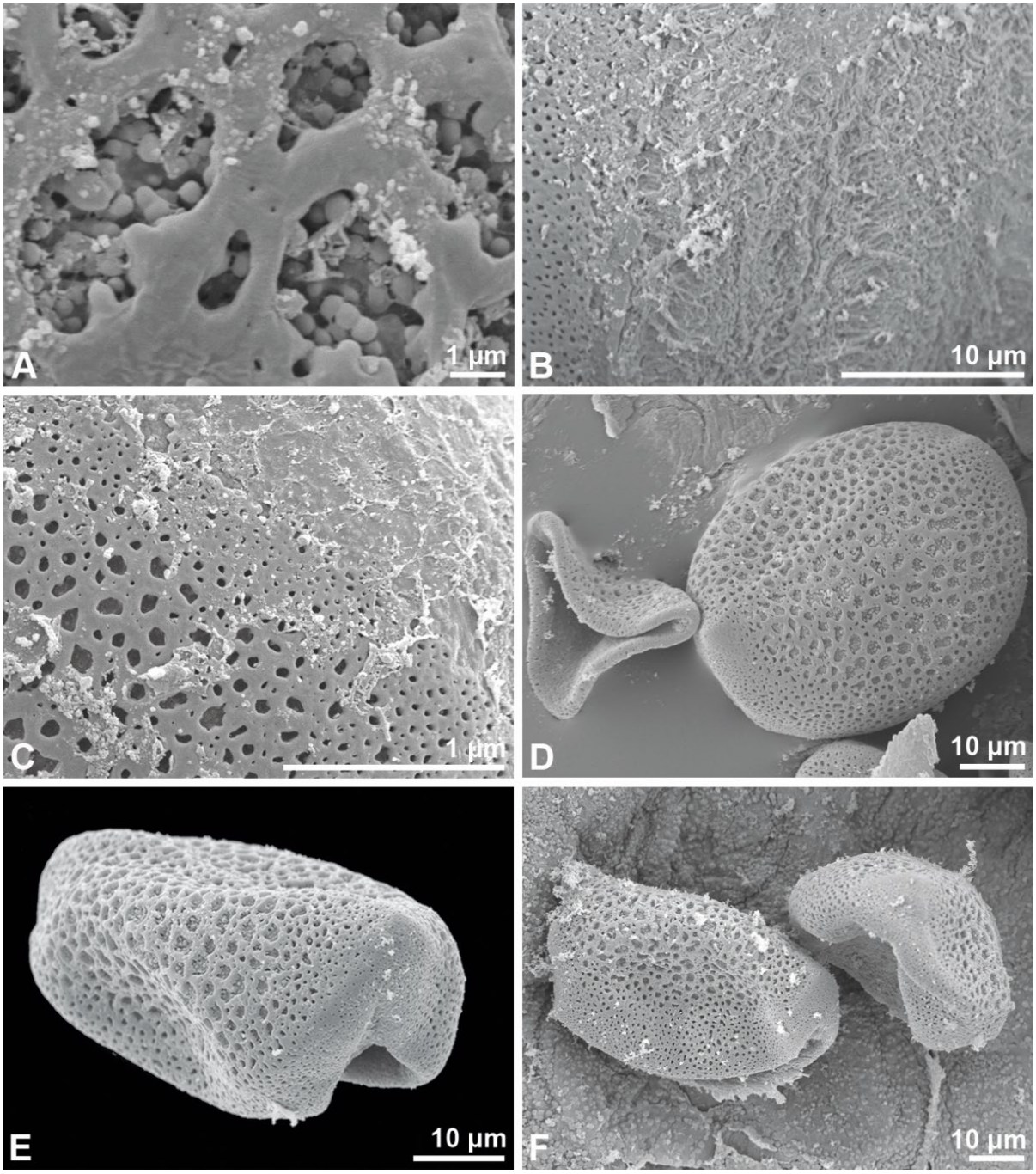

Figure 8: Scanning electron micrographs of *Agapanthus africanus* (DMP+CPD)

A. Detail of exine

B. Detail of aperture

C. Sulcus border

D. Overview showing dry (left) and semi-hydrated (right) pollen grains

E. Dry pollen grain boat-shaped

F. Overview of dry pollen grains attached to the inner anther wall with Ubisch bodies

Albuca bracteata (Asparagales, Asparagaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **elliptical**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **very large (>100 µm)**	Shape (Dry Pollen): **boat-shaped**
Pollen Class: **sulcate**	Outline in Polar View (Dry Pollen): **n/a**
Polarity: **heteropolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **1**	Aperture Peculiarities: **aperture membrane psilate**
Aperture Condition: **sulcate**	Ornamentation SEM: **microreticulate, perforate**
Aperture Type: **sulcus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

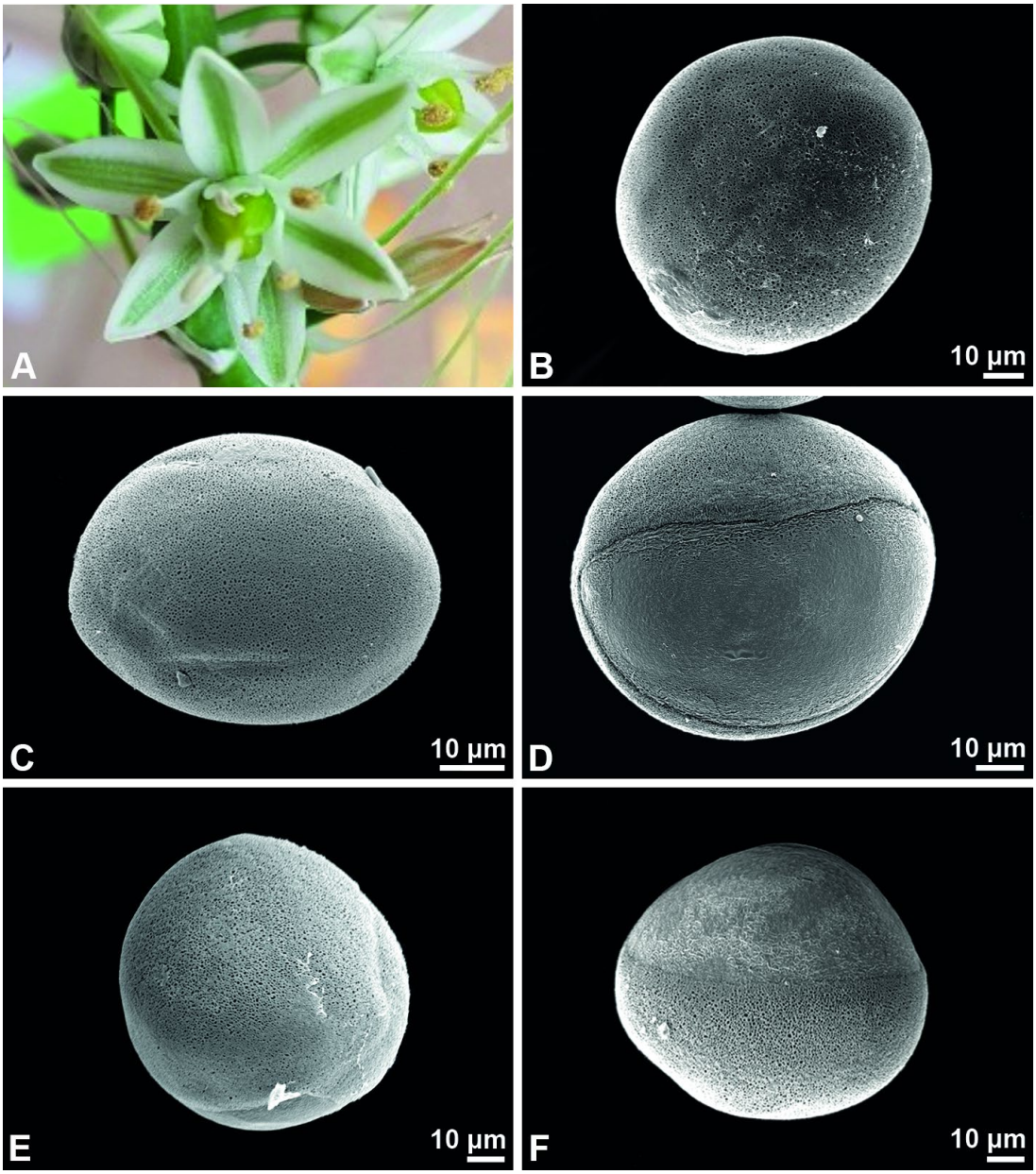

Figure 9: Plant image and scanning electron micrographs of *Albuca bracteata* (DMP+CPD)

A. Flowers

B. Hydrated pollen grain in oblique equatorial view (long axis)

C. Hydrated pollen grain in polar proximal view (long axis)

D. Hydrated pollen grain in oblique polar distal view (long axis)

E. Hydrated pollen grain in oblique equatorial view (short axis)

F. Hydrated pollen grain in equatorial view (long axis)

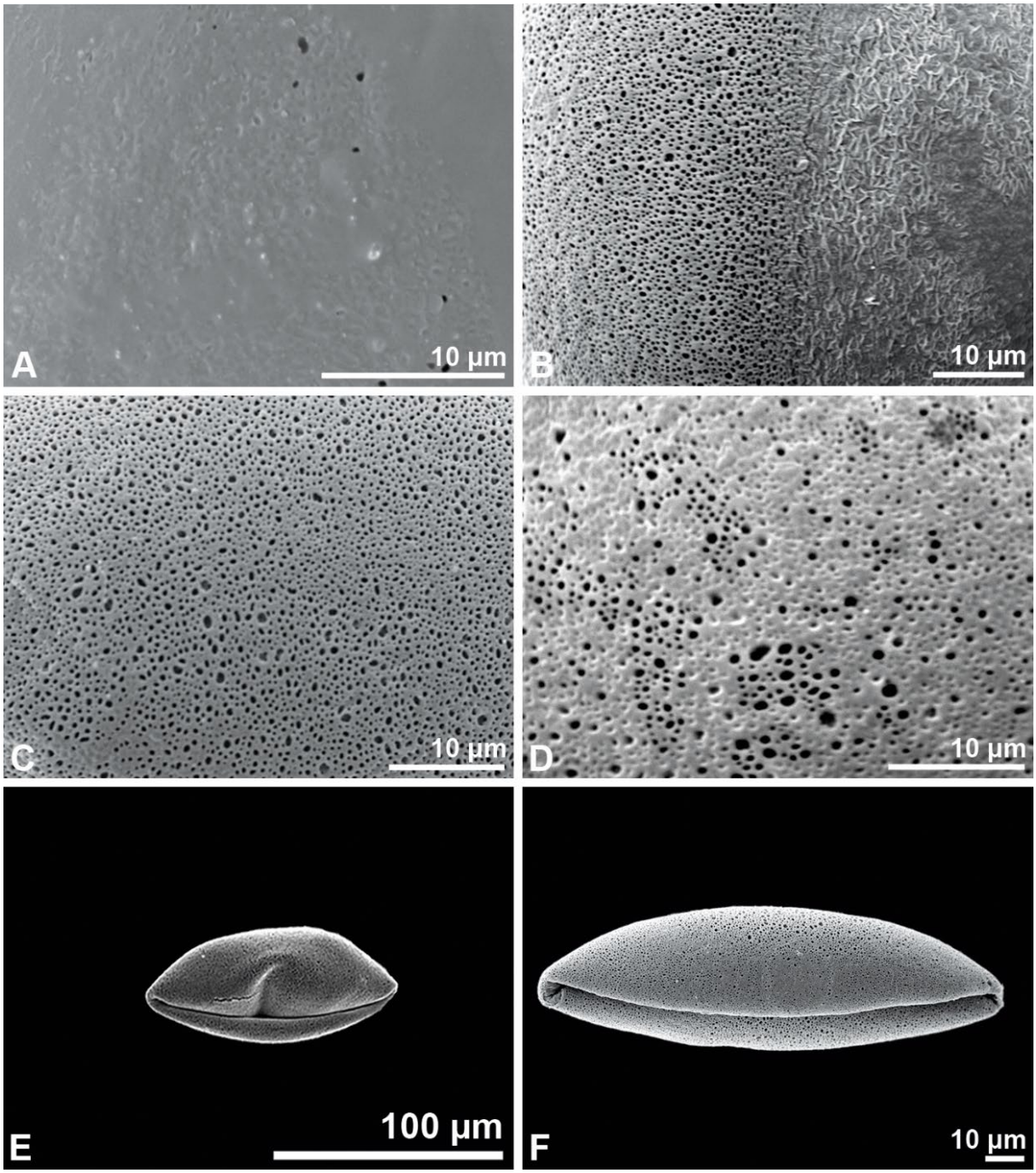

Figure 10: Scanning electron micrographs of *Albuca bracteata* (DMP+CPD)

A. Detail of the aperture

B. Sulcus border

C-D. Exine surface

E-F. Dry pollen boat-shaped

Iris missouriensis (Asparagales, Iridaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal to elliptical**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **large (51-100 µm)**	Shape (Dry Pollen): **boat-shaped**
Pollen Class: **sulcate**	Outline in Polar View (Dry Pollen): **elliptic**
Polarity: **heteropolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **1**	Aperture Peculiarities: **aperture membrane psilate**
Aperture Condition: **sulcate**	Ornamentation SEM: **reticulate, heterobrochate, free-standing columellae**
Aperture Type: **sulcus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **present**	

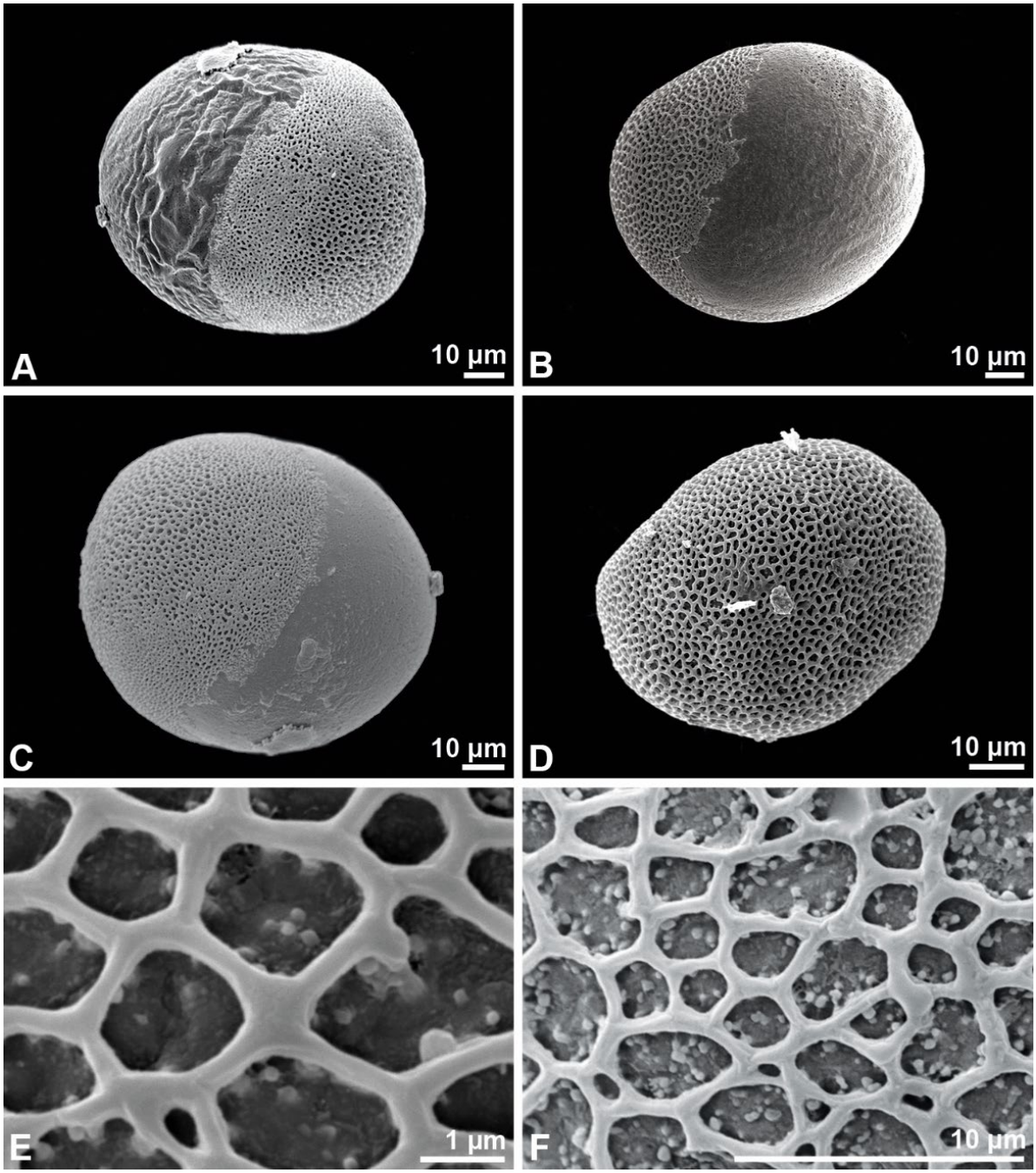

Figure 11: Scanning electron micrographs of *Iris missouriensis* (DMP+CPD)

A. Hydrated pollen grain in equatorial view (long axis)

B. Hydrated pollen grain in oblique equatorial view

C. Hydrated pollen grain in equatorial view (long axis)

D. Hydrated pollen grain in polar proximal view

E-F. Exine surface

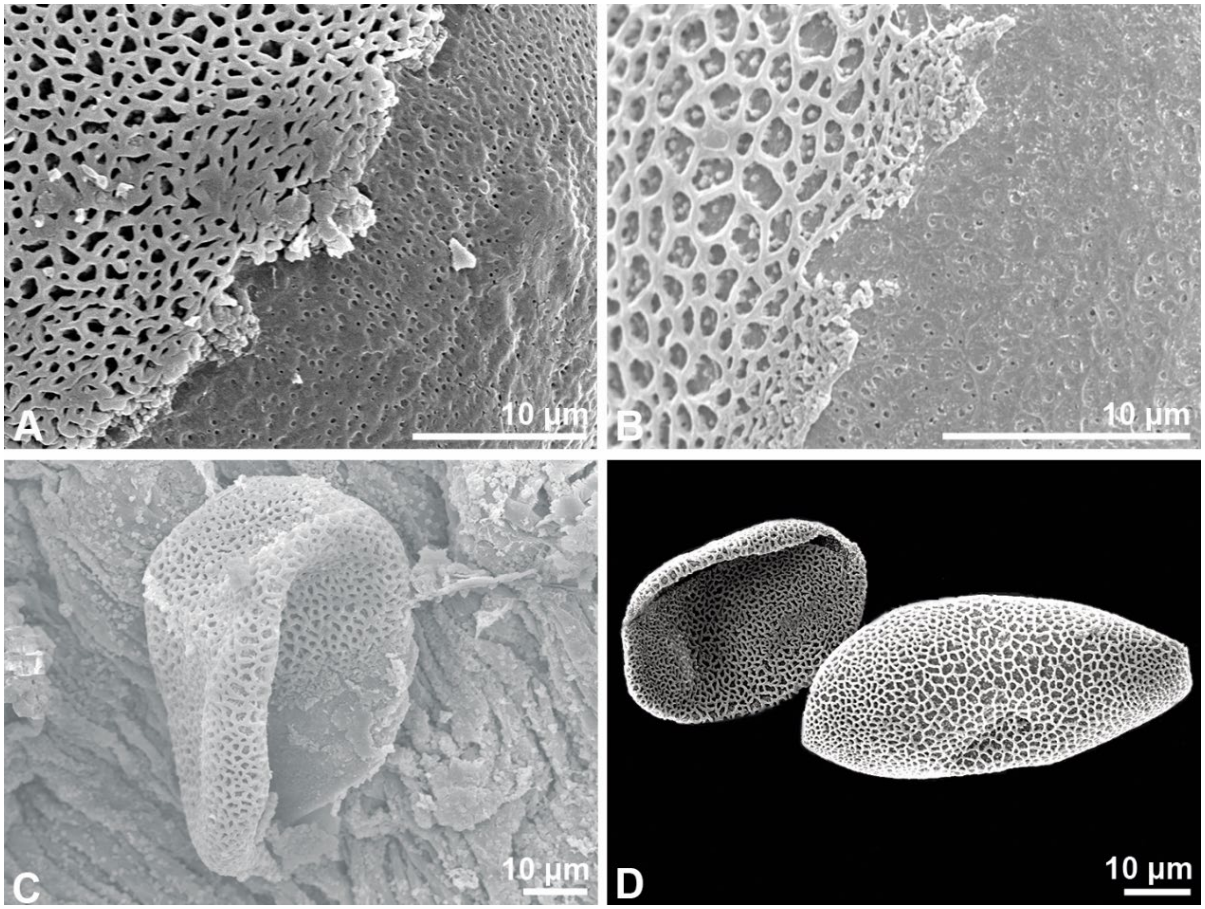

Figure 12: Scanning electron micrographs of *Iris missouriensis* (DMP+CPD)

A-B. Sulcus border

C. Dry pollen grain attached to the inner anther wall with Ubisch bodies

D. Dry pollen grains boat-shaped

Reseda alba (Brassicales, Resedaceae)

Pollen description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **small (10-25 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **colporate**	Outline in Polar View (Dry Pollen): **lobate**
Polarity: **isopolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **aperture membrane psilate**
Aperture Condition: **colporate, tricolporate**	Ornamentation SEM: **reticulate**
Aperture Type: **colporus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

Annotations
The colpi are long with distinct margin. The pori are almost as big as the colpi and can only be clearly seen in dry condition. In hydrated condition pollen may therefore be misinterpreted as colpate**.**

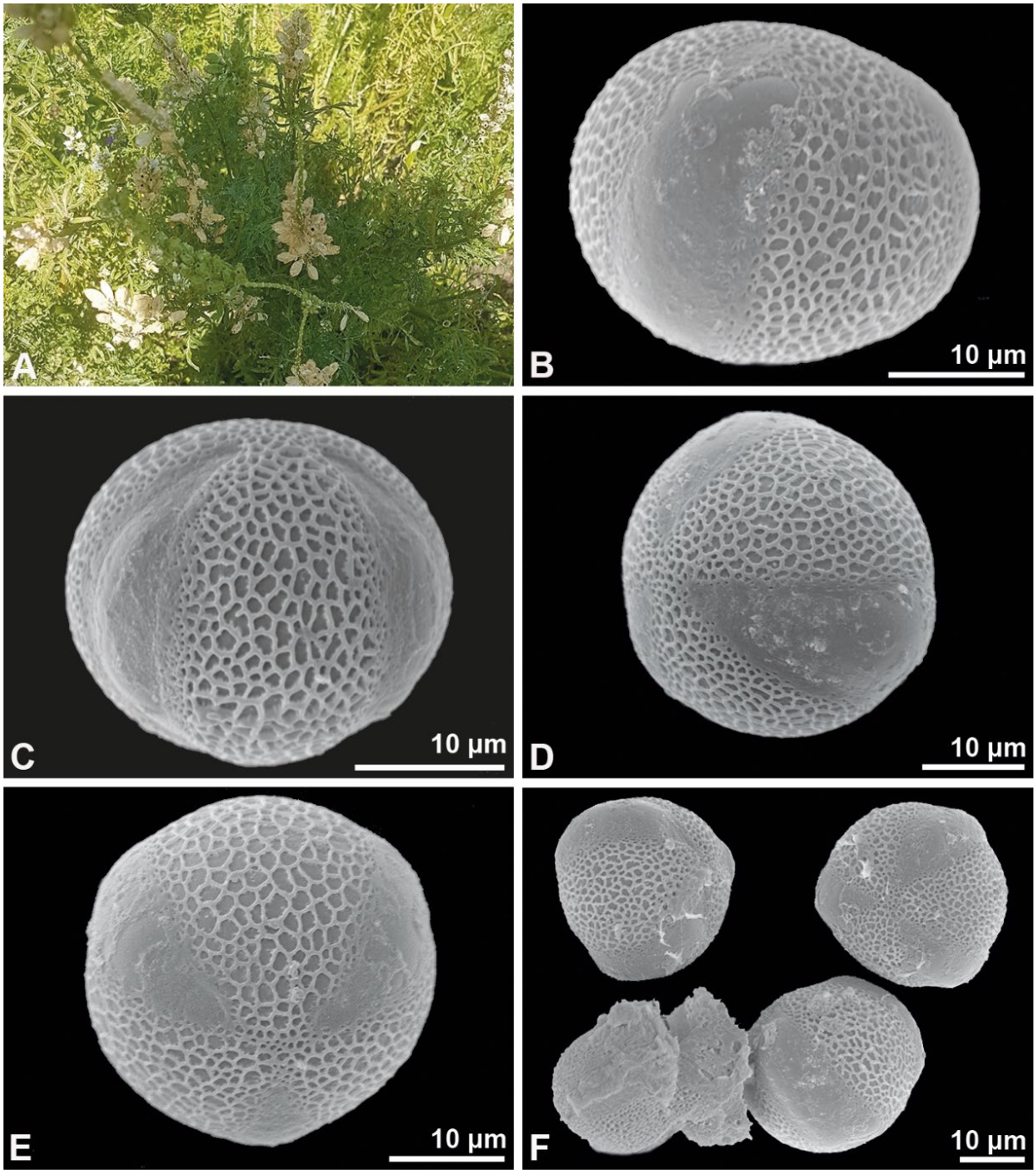

Figure 13: Plant image and scanning electron micrographs of *Reseda alba* (DMP+CPD)

A. Habitus

B-C. Hydrated pollen grain in equatorial view

D. Hydrated pollen grain in oblique view

E. Hydrated pollen grain in polar view

F. Hydrated pollen grains in the overview

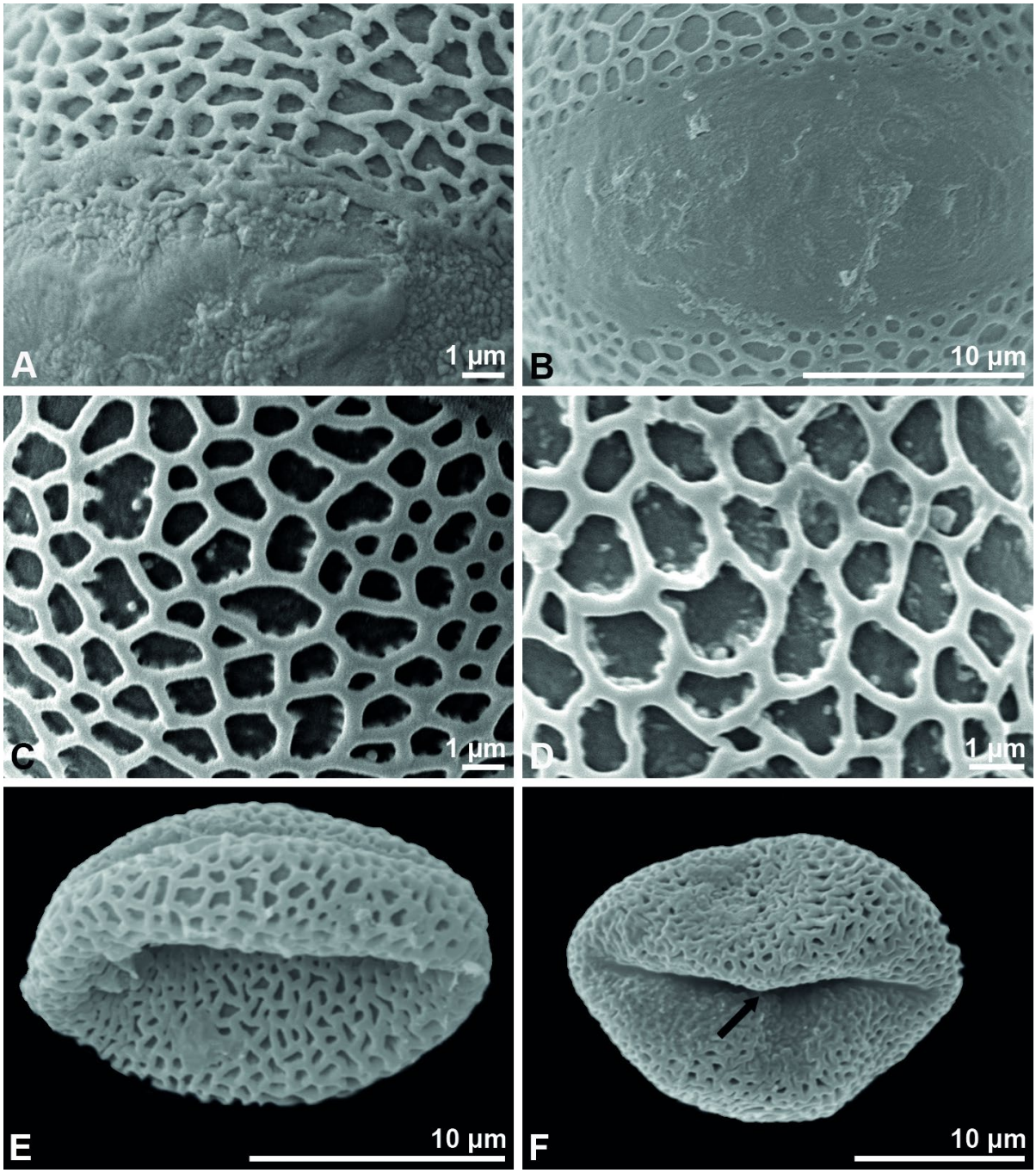

Figure 14: Scanning electron micrographs of *Reseda alba* (DMP+CPD)

A-B. Detail of aperture

C-D. Exine surface

E-F. Overview showing dry pollen with indistinct porus (**F,** arrow)

Rivina humilis (Caryophyllales, Petiveriaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **medium-sized (26-50 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **pantocolpate**	Outline in Polar View (Dry Pollen): **irregular**
Polarity: **n/a**	Infoldings (Dry Pollen): **irregularly infolded**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **n/a**

Aperture and Ornamentation	
Aperture Number: **>6**	Aperture Peculiarities: **aperture membrane psilate**
Aperture Condition: **pantocolpate**	Ornamentation SEM: **psilate, perforate, foveolate, microechinate**
Aperture Type: **colpus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

Annotations
On hydrated pollen grains, the microechini are often covered by remnants of the tapetum/locular fluid and are only clearly visible on dry pollen grains.

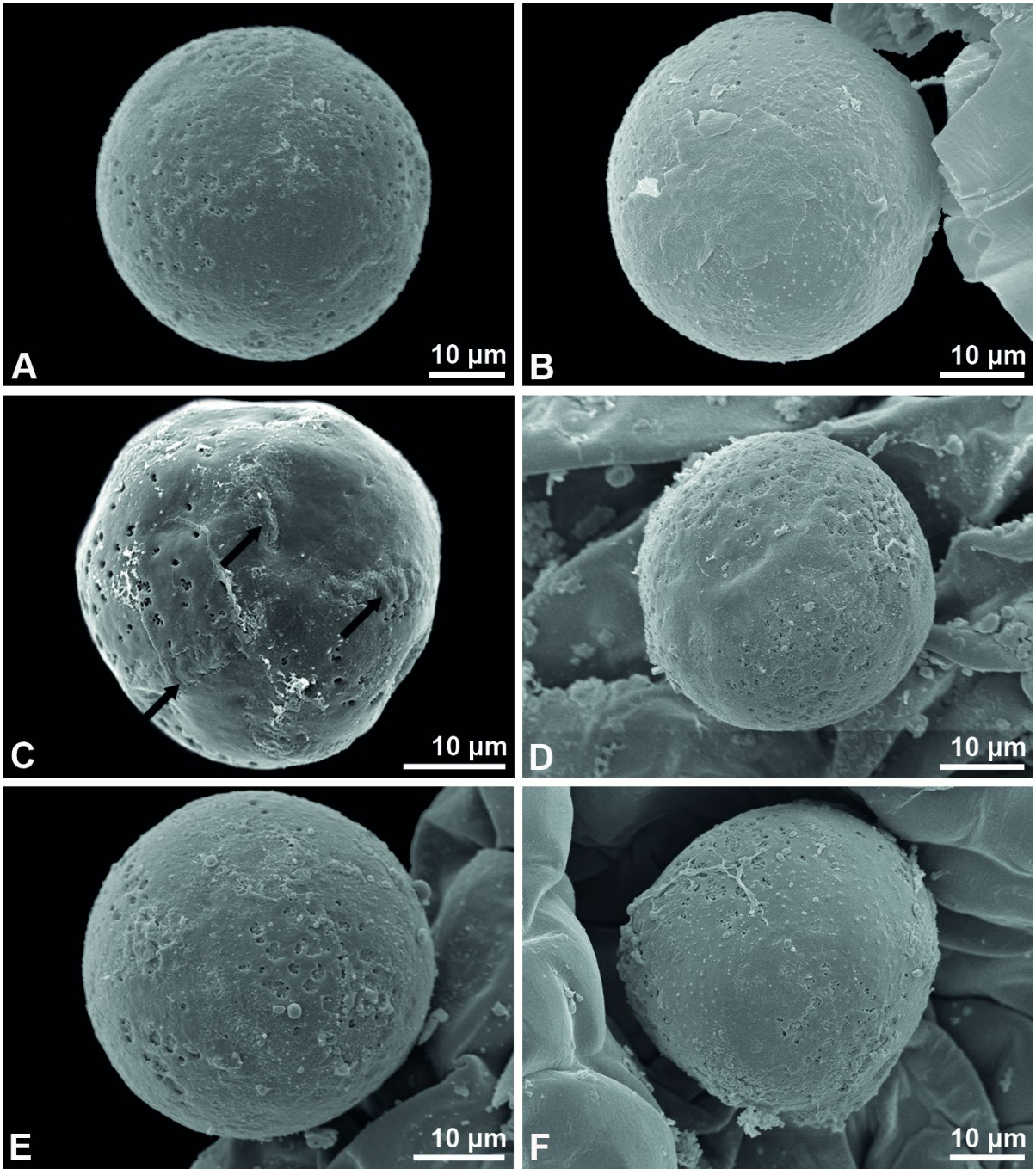

Figure 15: Scanning electron micrographs of *Rivina humilis* (DMP+CPD)

A-B. Hydrated pollen grain in overview, apertures not visible

C-D. Details of apertures (arrows)

E-F. Hydrated pollen grain attached to the inner anther wall; apertures not visible

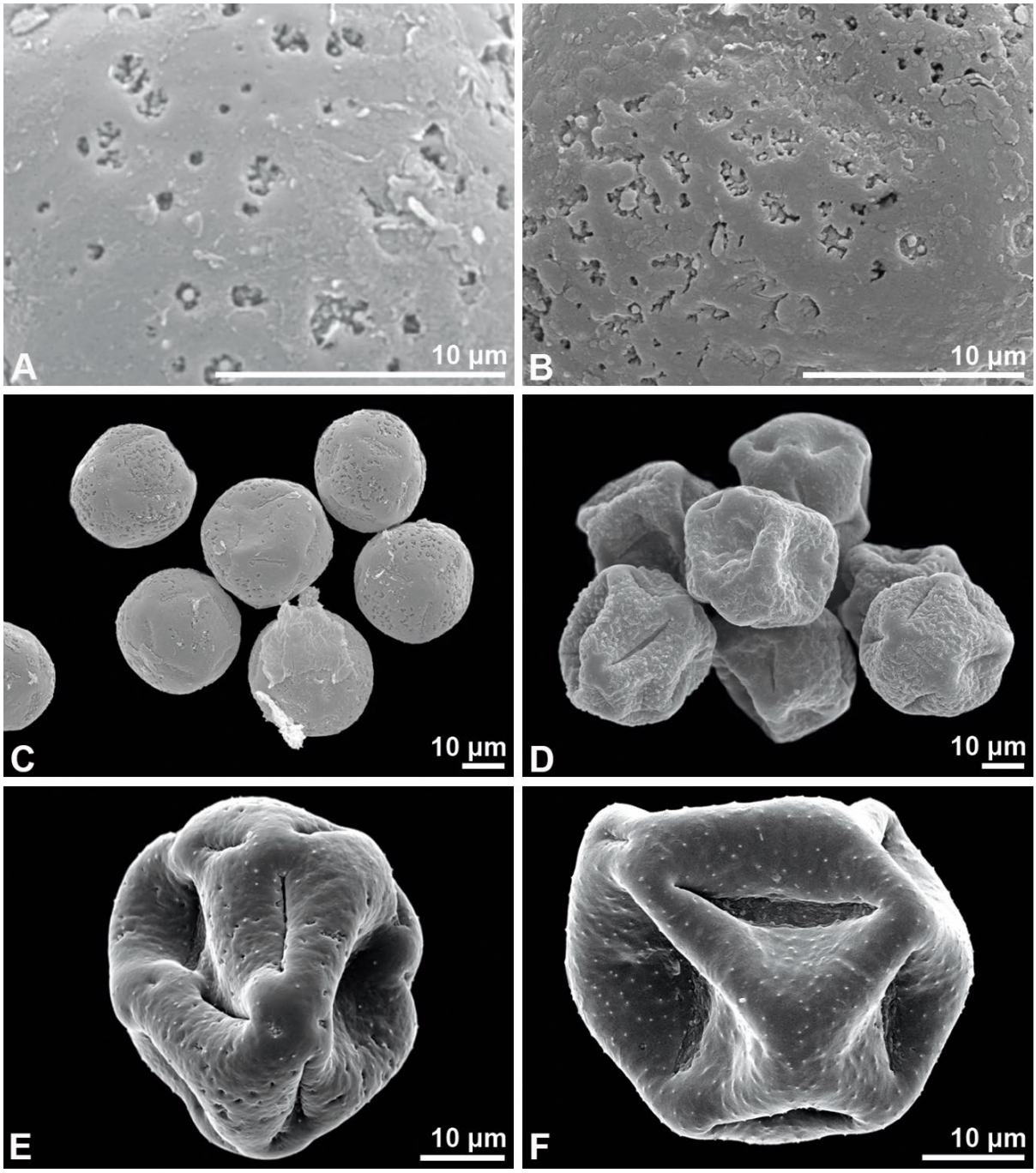

Figure 16: Scanning electron micrographs of *Rivina humilis* (DMP+CPD)

A-B. Exine surface

C. Hydrated pollen grains in the overview

D. Semi-hydrated pollen grains in the overview

E-F. Dry pollen grains in the overview

Telephium imperati (Caryophyllales, Caryophyllaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **large (51-100 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **colpate**	Outline in Polar View (Dry Pollen): **lobate**
Polarity: **isopolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **prolate**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **colpate, tricolpate**	Ornamentation SEM: **perforate, nanoechinate**
Aperture Type: **colpus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **present**	

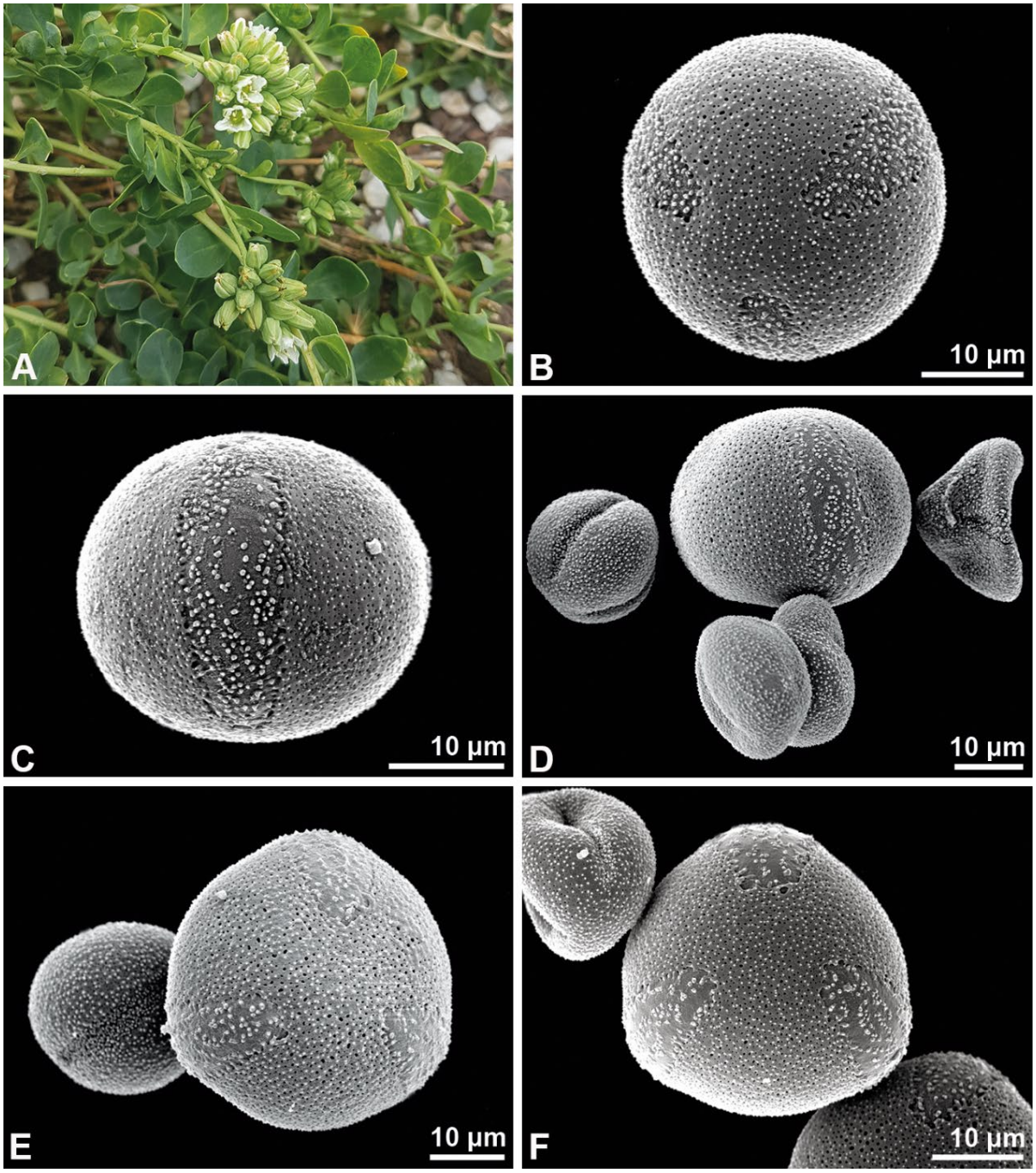

Figure 17: Plant image and scanning electron micrographs of *Telephium imperati* (DMP+CPD)

A. Habitus of plant and inflorescences

B. Hydrated pollen grain in polar view

C. Hydrated pollen grain in equatorial view

D. Hydrated (center), semi-hydrated (left side), and dry (right side) pollen in the overview

E-F. Hydrated (right) and small semi-hydrated (left) pollen in the overview

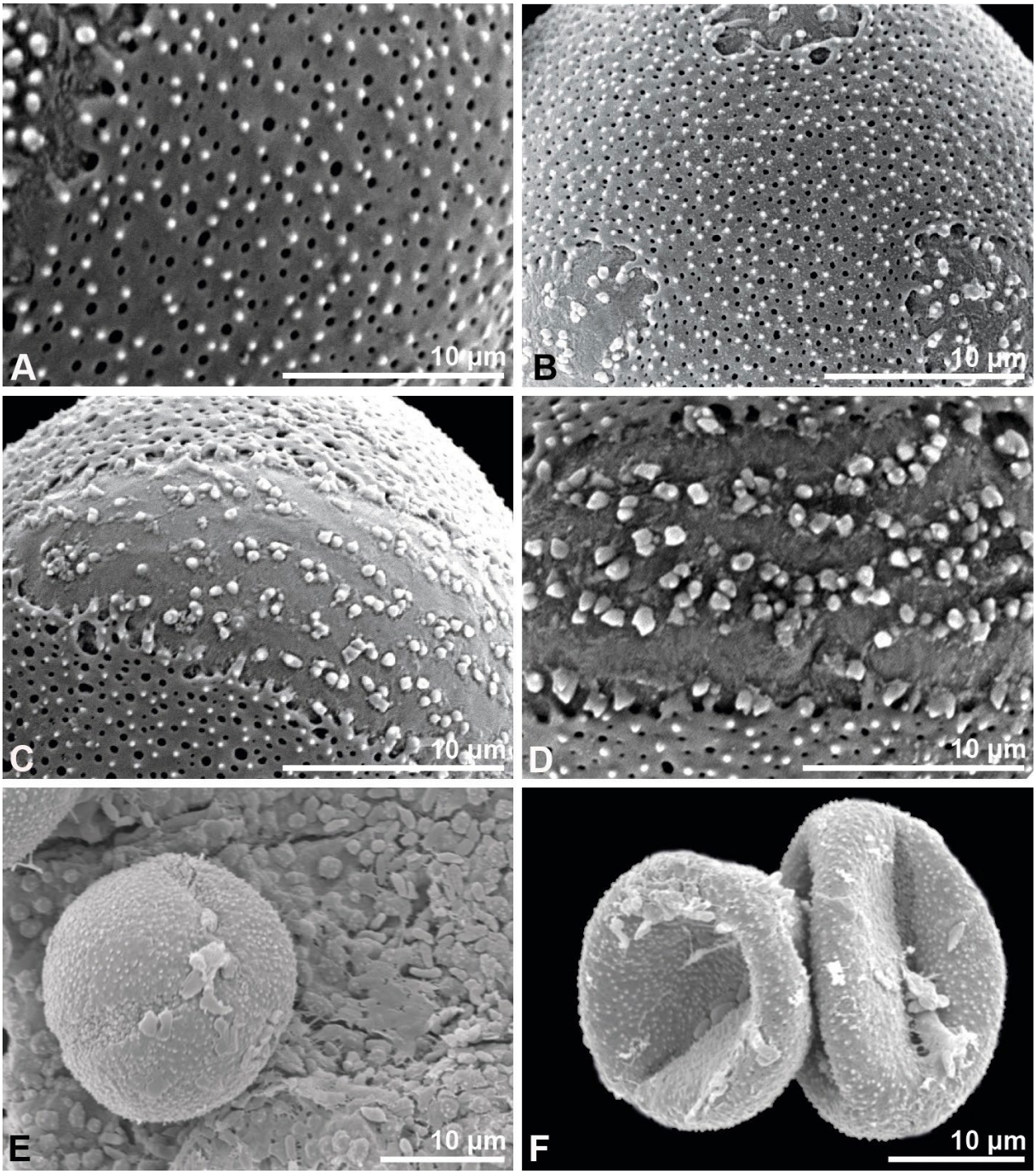

Figure 18: Scanning electron micrographs of *Telephium imperati* (DMP+CPD)

A-B. Detail of exine

C-D. Detail of aperture

E. Semi-hydrated pollen grain attached to the inner anther wall with Ubisch bodies

F. Dry pollen grains in the overview, with remnants from locular fluid and/or pollen coatings

Tradescantia spathacea (Commelinales, Commelinaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **elliptical**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **medium-sized (26-50 µm)**	Shape (Dry Pollen): **boat-shaped**
Pollen Class: **sulcate**	Outline in Polar View (Dry Pollen): **n/a**
Polarity: **heteropolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **oblate**

Aperture and Ornamentation	
Aperture Number: **1**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **sulcate**	Ornamentation SEM: **microverrucate, perforate**
Aperture Type: **sulcus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

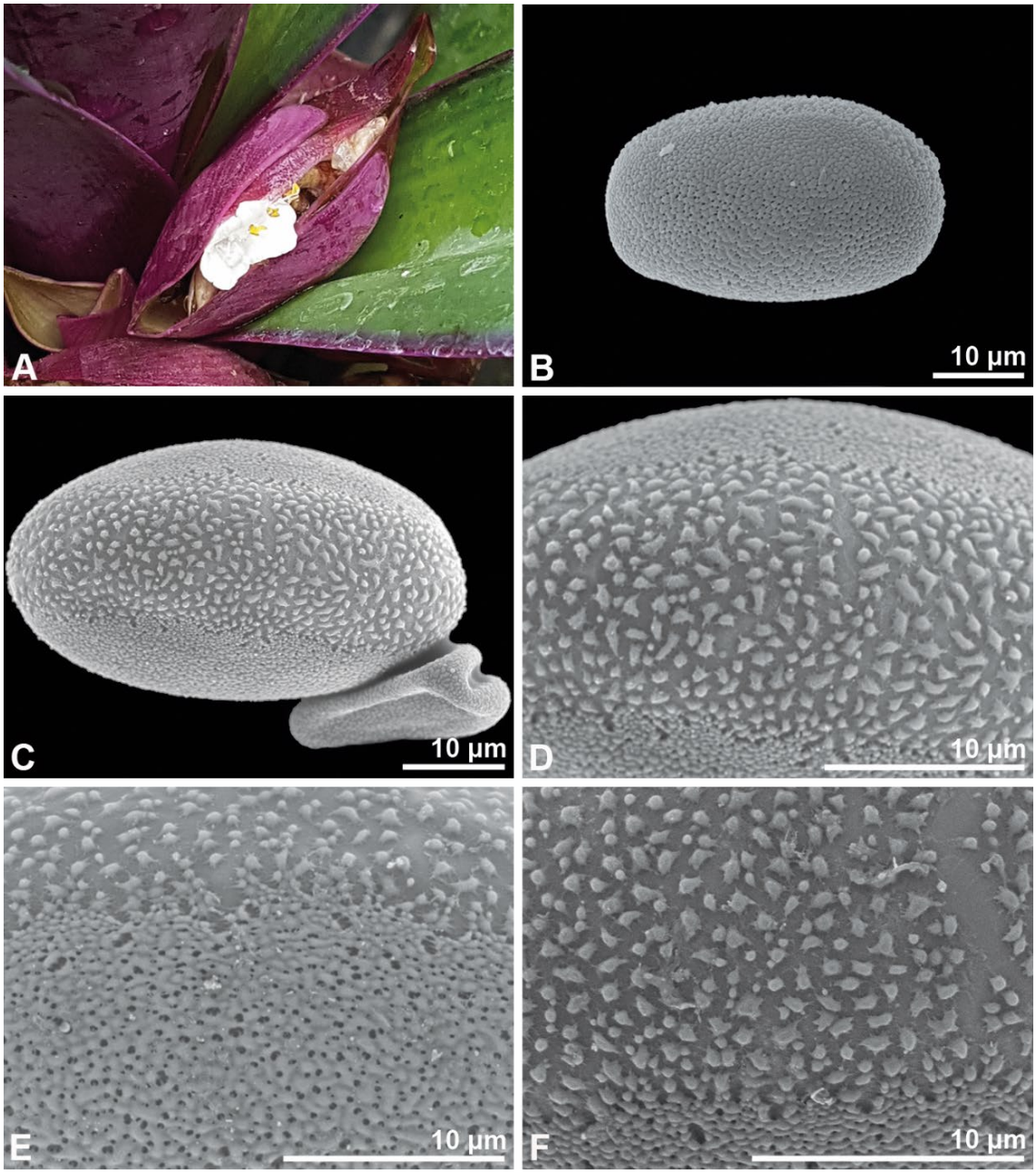

Figure 19: Plant image and scanning electron micrographs of *Tradescantia spathacea* (DMP+CPD)

A. Flower

B. Hydrated pollen grain in equatorial view (long axis)

C. Overview showing distal polar view of hydrated (left) and dry (right) pollen in oblique view

D. Detail of aperture

E. Sulcus border

F. Detail of aperture

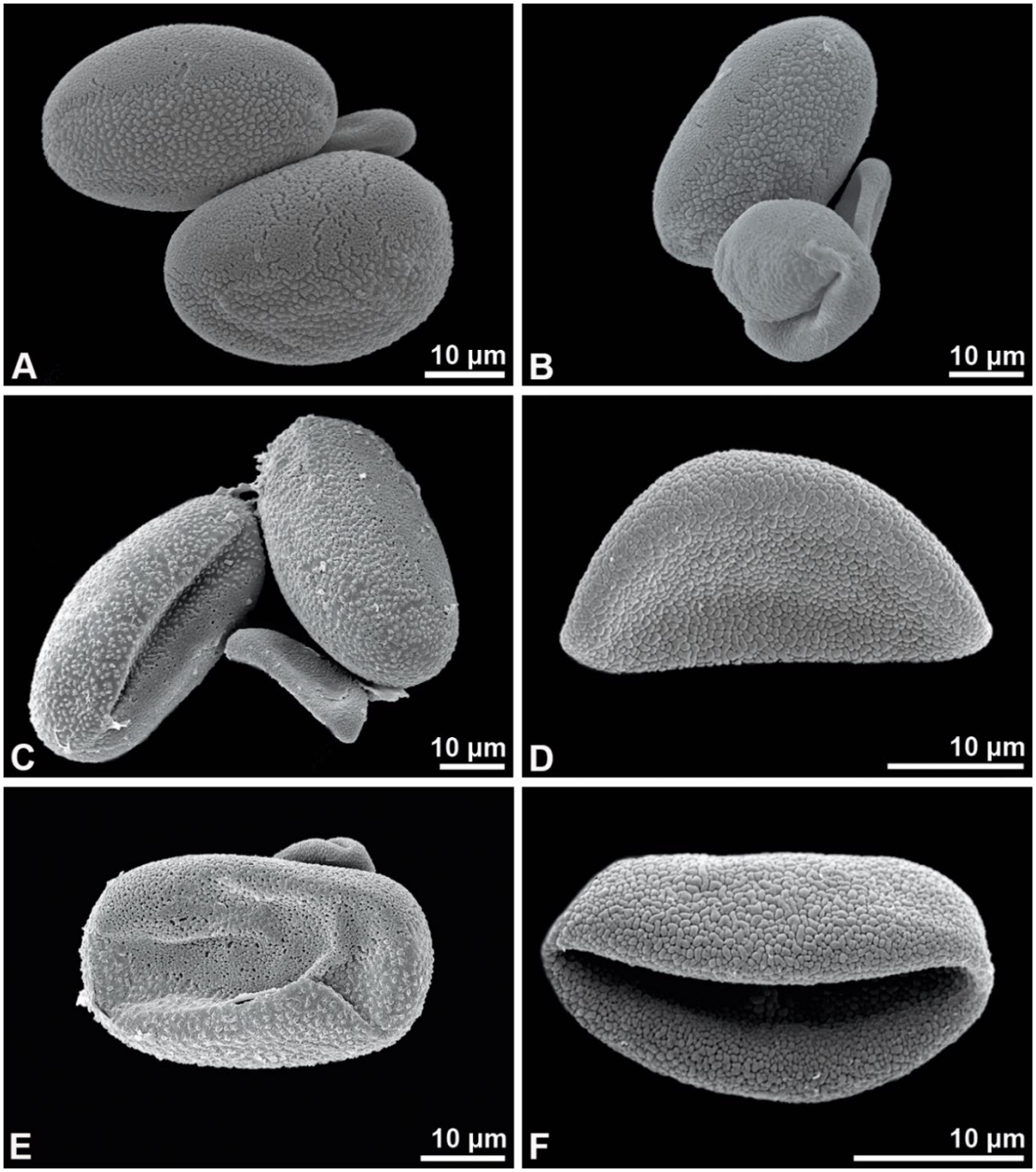

Figure 20: Scanning electron micrographs of *Tradescantia spathacea* (DMP+CPD)

A. Hydrated pollen grains in overview, with small degenerated dry pollen grain attached

B. Hydrated pollen, semi-hydrated pollen (below), and degenerated pollen grain (right side)

C. Semi-hydrated pollen grains, with small, degenerated pollen grain attached

D-F. Dry pollen boat-shaped in equatorial view (**D-E**, long axis) and polar distal view (**F**)

Geranium sanguineum (Geraniales, Geraniaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **large (51-100 µm)**	Shape (Dry Pollen): **irregular**
Pollen Class: **colporate**	Outline in Polar View (Dry Pollen): **irregular**
Polarity: **isopolar**	Infoldings (Dry Pollen): **irregularly infolded**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **n/a**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **brevicolporus**
Aperture Condition: **tricolporate**	Ornamentation SEM: **reticulate, clavate**
Aperture Type: **colporus**	Suprasclupture SEM: **clavate**

Miscellaneous	
Pollen Coatings: **present**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

Annotations

Colpus is almost not visible in hydrated conditions.

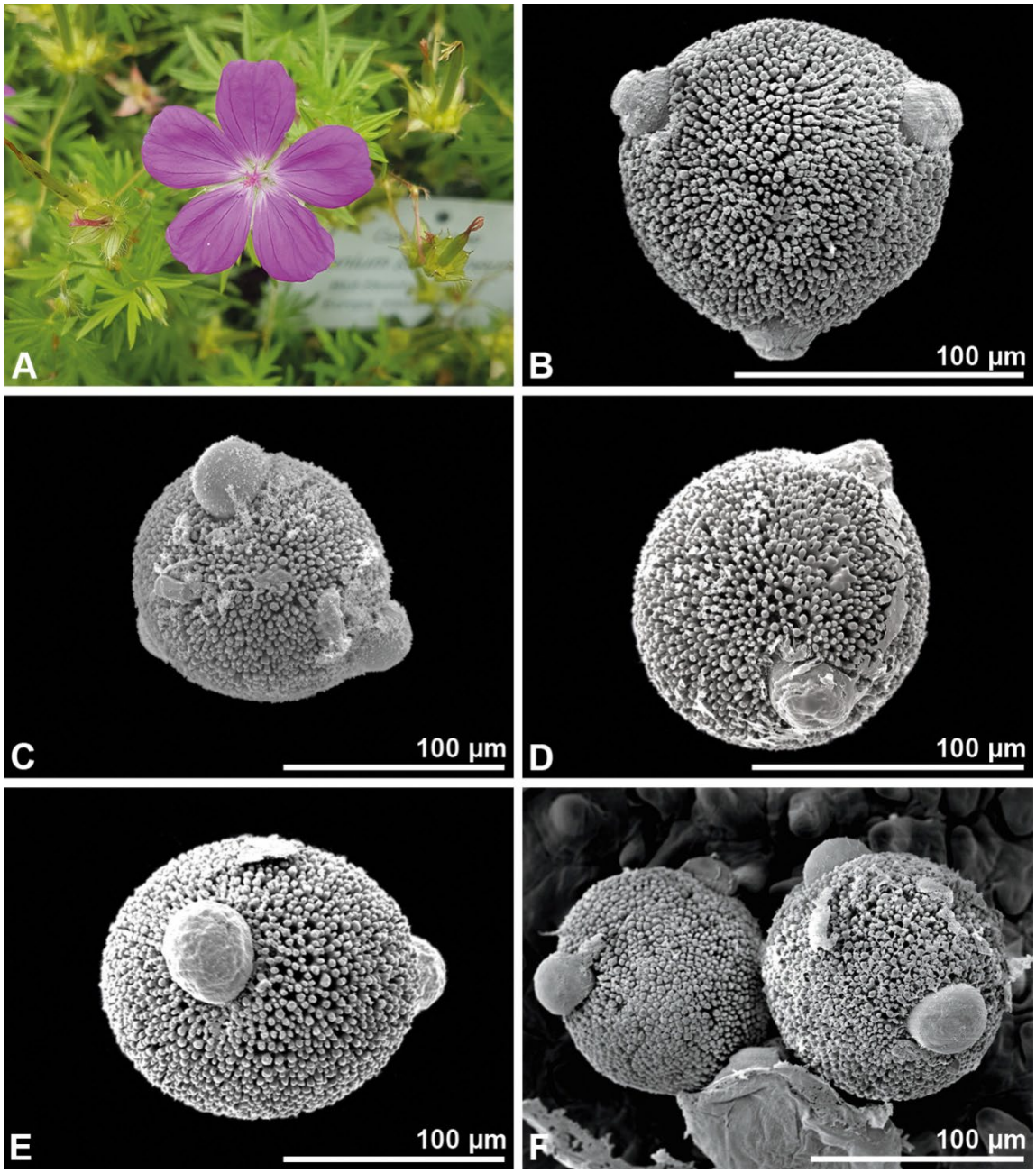

Figure 21: Plant image and scanning electron micrographs of *Geranium sanguineum* (DMP+CPD)

A. Flower

B. Hydrated pollen grain in polar view

C-D. Hydrated pollen grain in oblique view

E. Hydrated pollen grain in equatorial view

F. Pollen grains attached to the inner anther wall, and pollenkitt attached to exine surface

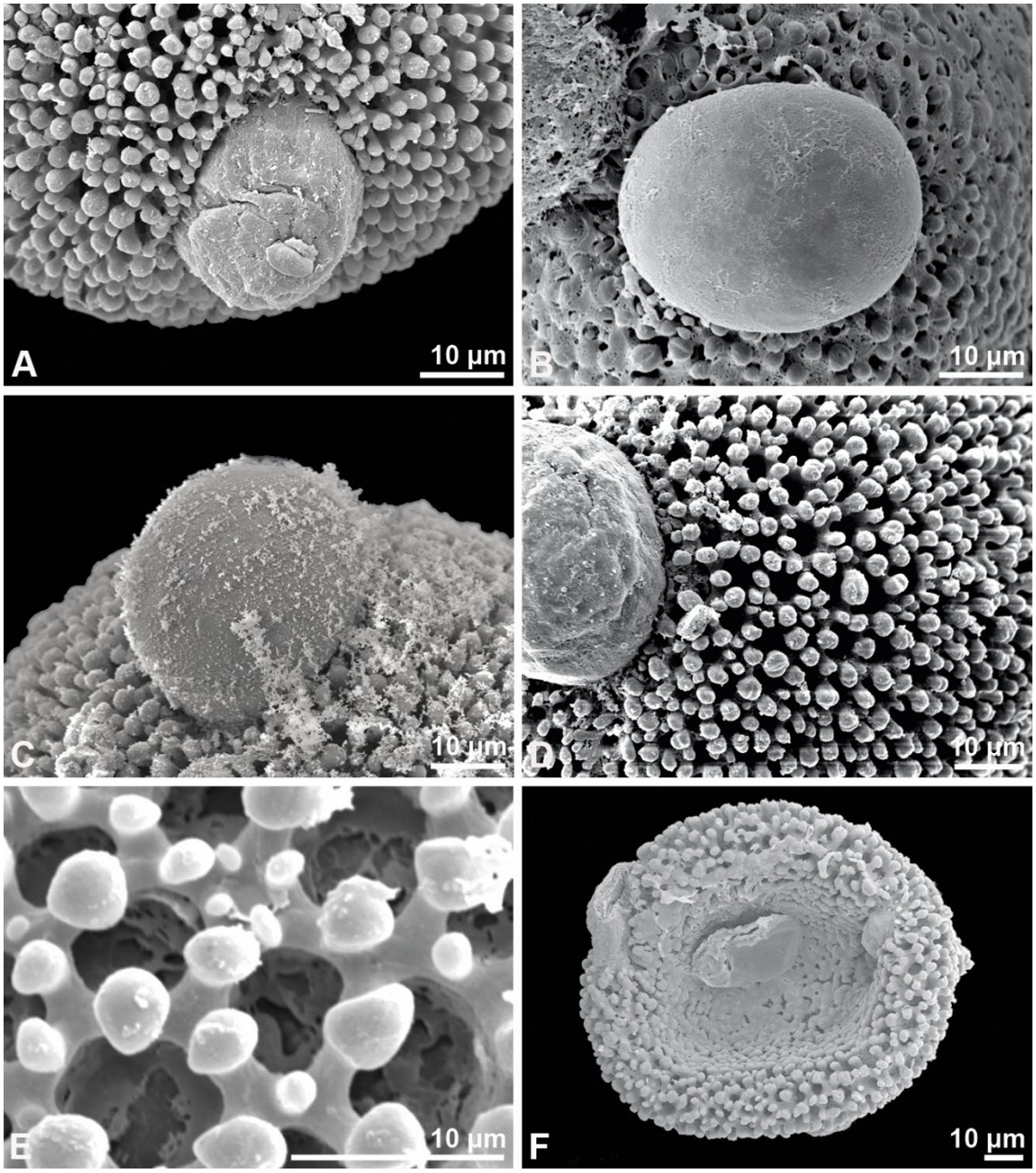

Figure 22: Scanning electron micrographs of *Geranium sanguineum* (DMP+CPD)

A-C. Aperture in the overview, only porus visible in SEM

D-E. Exine surface

F. Dry pollen grain

Jacaranda mimosifolia (Lamiales, Bignoniaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **medium-sized (26-50 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **colporate**	Outline in Polar View (Dry Pollen): **lobate**
Polarity: **isopolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **prolate**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **colporate, tricolporate**	Ornamentation SEM: **perforate, psilate**
Aperture Type: **colporus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **present**	

Annotations
The colporus is sometimes not clearly visible.

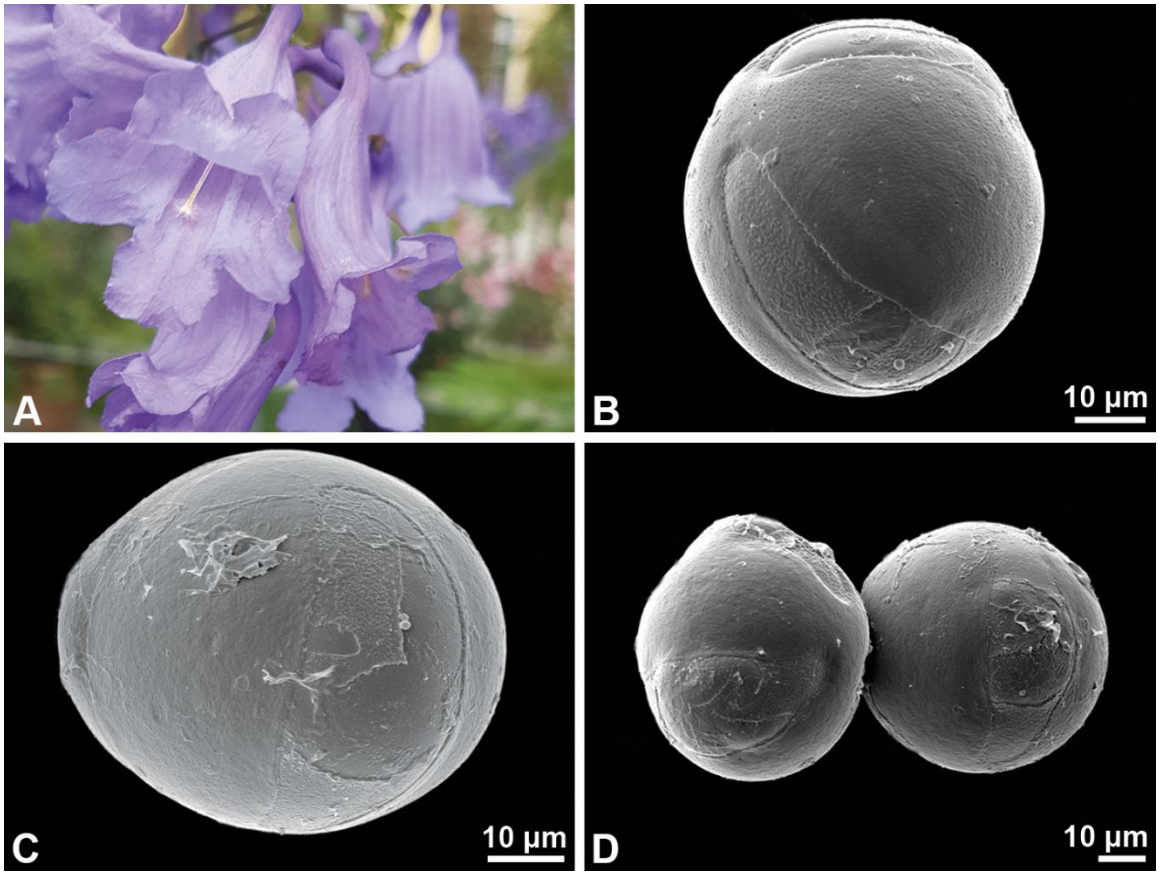

Figure 23: Plant image and scanning electron micrographs of *Jacaranda mimosifolia* (DMP+CPD)

A. Flowers

B. Hydrated pollen grain in oblique view

C. Hydrated pollen grain in equatorial view

D. Hydrated pollen grains in oblique view (left) and equatorial view (right)

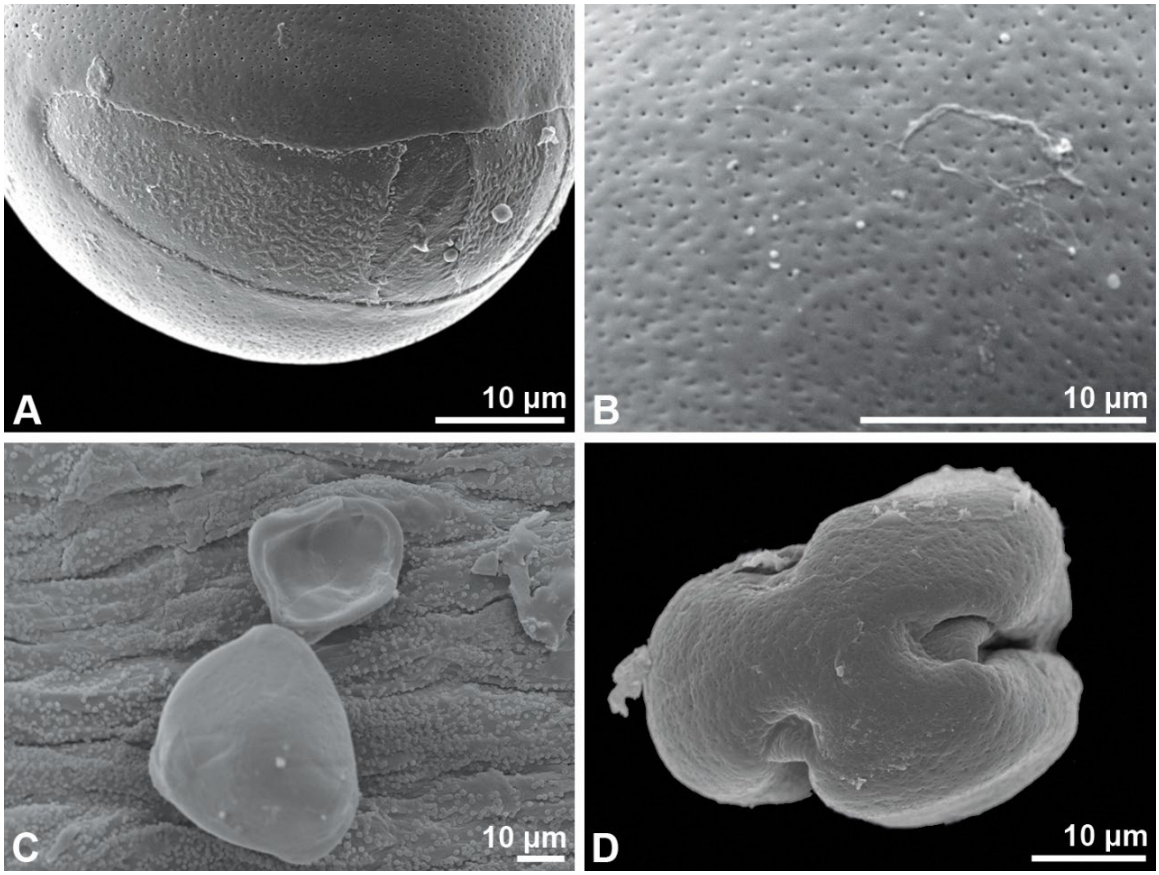

Figure 24: Scanning electron micrographs of *Jacaranda mimosifolia* (DMP+CPD)

A. Overview of aperture

B. Exine surface

C. Semi-hydrated pollen (proximal side) and sterile pollen grain attached to the inner anther wall, Ubisch bodies present

D. Dry pollen grain in polar view

Perilla frutescens (Lamiales, Lamiaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **n/a**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **elliptic**
Size (Pollen Unit): **medium-sized (26-50 µm)**	Shape (Dry Pollen): **disc-shaped**
Pollen Class: **colpate**	Outline in Polar View (Dry Pollen): **elliptic**
Polarity: **isopolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **prolate**
Aperture and Ornamentation	
Aperture Number: **6**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **hexacolpate, stephanoaperturate**	Ornamentation SEM: **reticulate, bireticulate**
Aperture Type: **colpus**	
Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

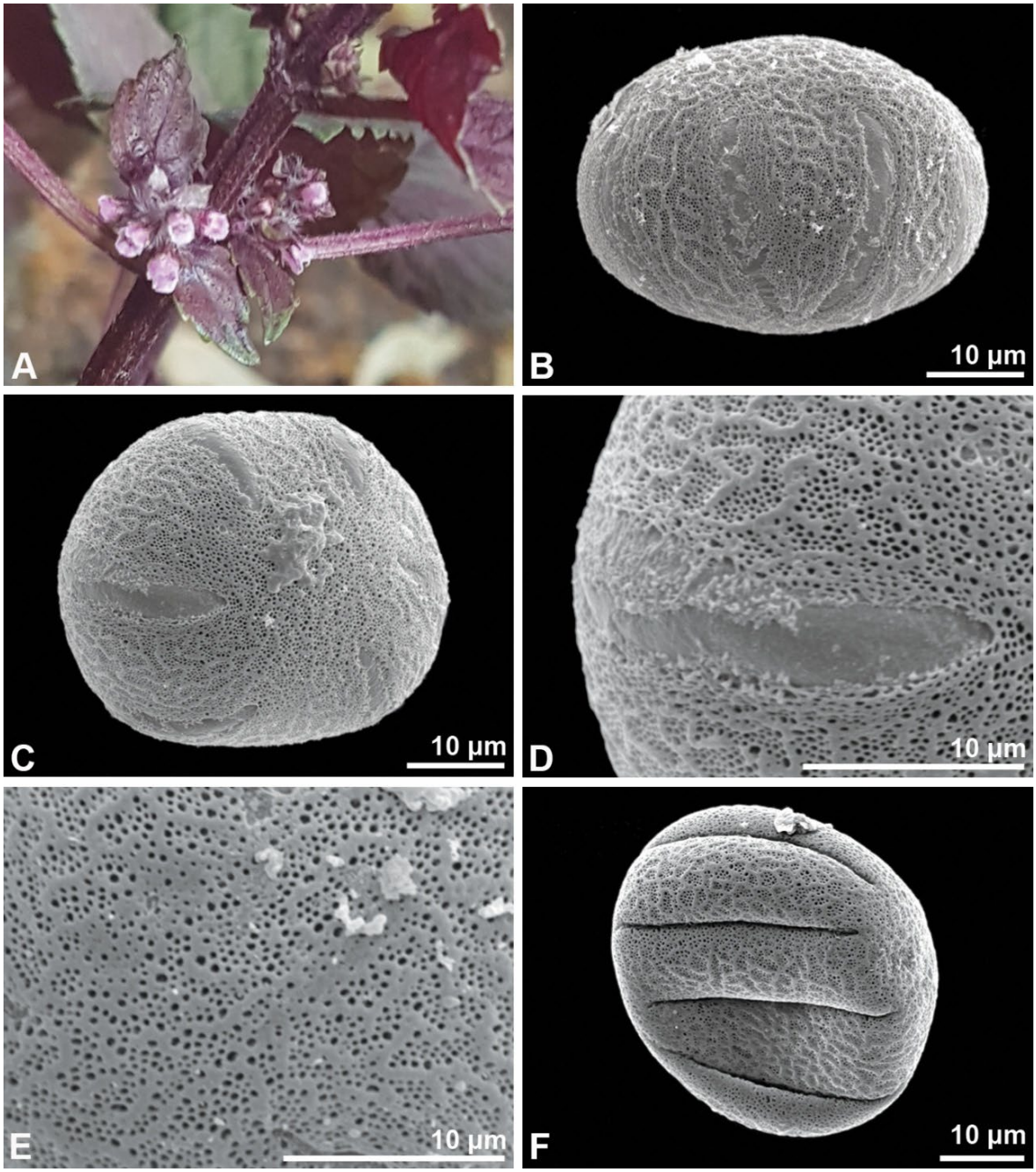

Figure 25: Plant image and scanning electron micrographs of *Perilla frutescens* (DMP+CPD)

A. Flowers

B. Hydrated pollen grain in equatorial view

C. Hydrated pollen grain in polar view

D. Detail of aperture

E. Exine surface

F. Dry pollen grain

Dalechampia spathulata (Malpighiales, Euphorbiaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **medium-sized (25-50 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **colporate**	Outline in Polar View (Dry Pollen): **lobate**
Polarity: **isopolar**	Infoldings (Dry Pollen): **irregularly infolded**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **prolate**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **brevicolpus**
Aperture Condition: **tricolporate**	Ornamentation SEM: **reticulate, free-standing columellae, heterobrochate**
Aperture Type: **colporus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

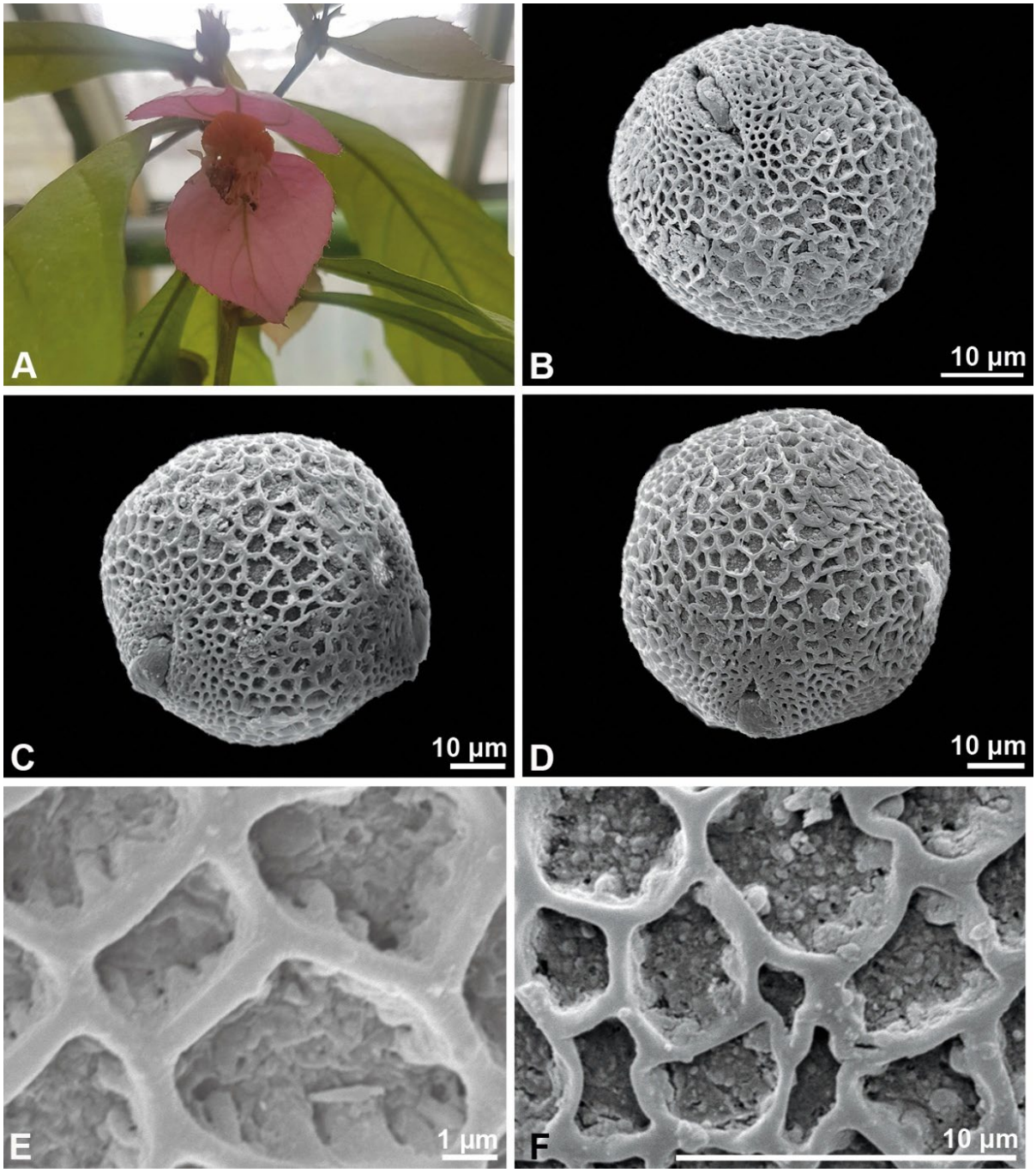

Figure 26: Plant image and scanning electron micrographs of *Dalechampia spathulata* (DMP+CPD)

A. Inflorescence (pseudanthium)

B. Hydrated pollen grain in oblique equatorial view

C-D. Hydrated pollen grain in oblique polar view

E-F. Exine surface

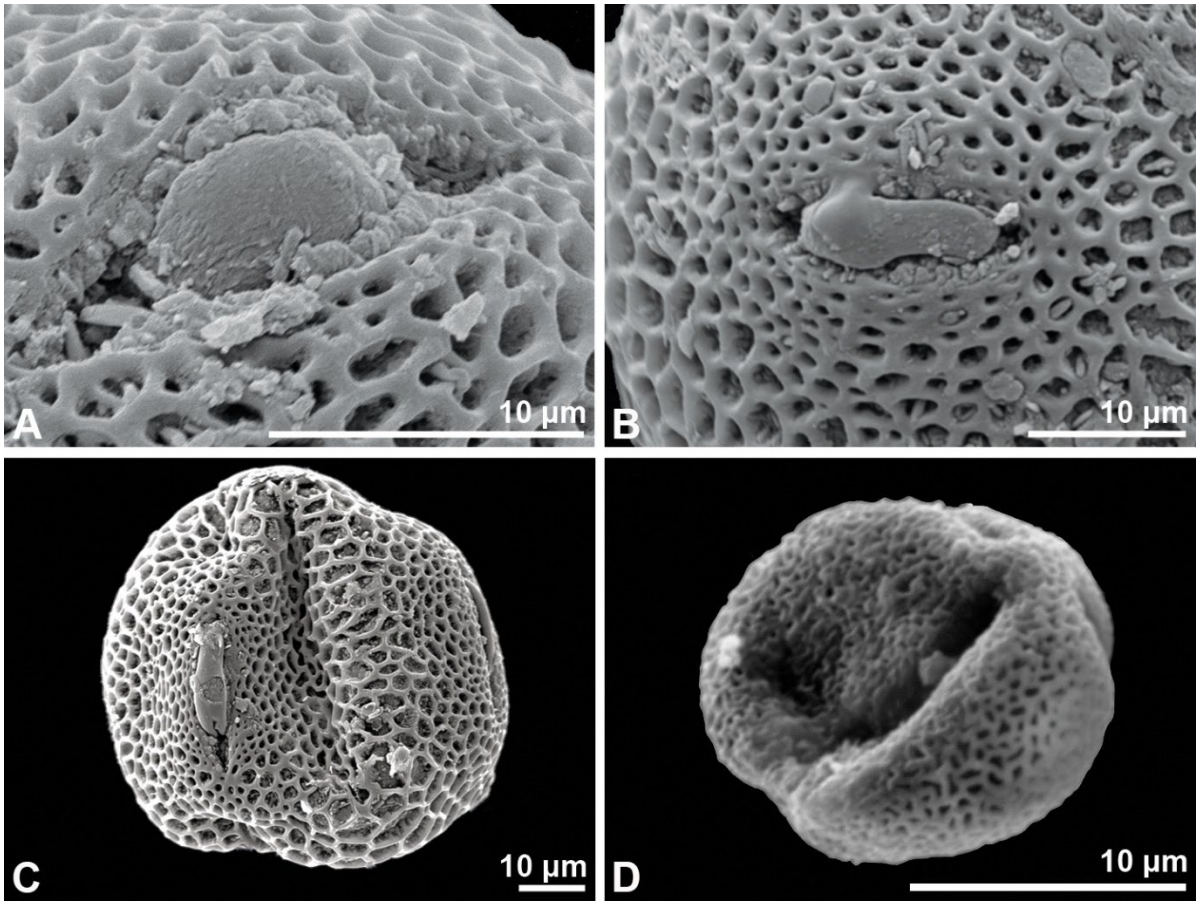

Figure 27: Scanning electron micrographs of *Dalechampia spathulata* (DMP+CPD)

A-B. Overview of aperture

C-D. Semi-hydrated pollen grains in equatorial view

Aquilegia canadensis (Ranunculales, Ranunculaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **medium-sized (26-50 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **colpate**	Outline in Polar View (Dry Pollen): **lobate**
Polarity: **isopolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **oblate**	P/E-Ratio (Dry Pollen): **prolate**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **colpate, tricolpate**	Ornamentation SEM: **perforate, nanoechinate**
Aperture Type: **colpus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

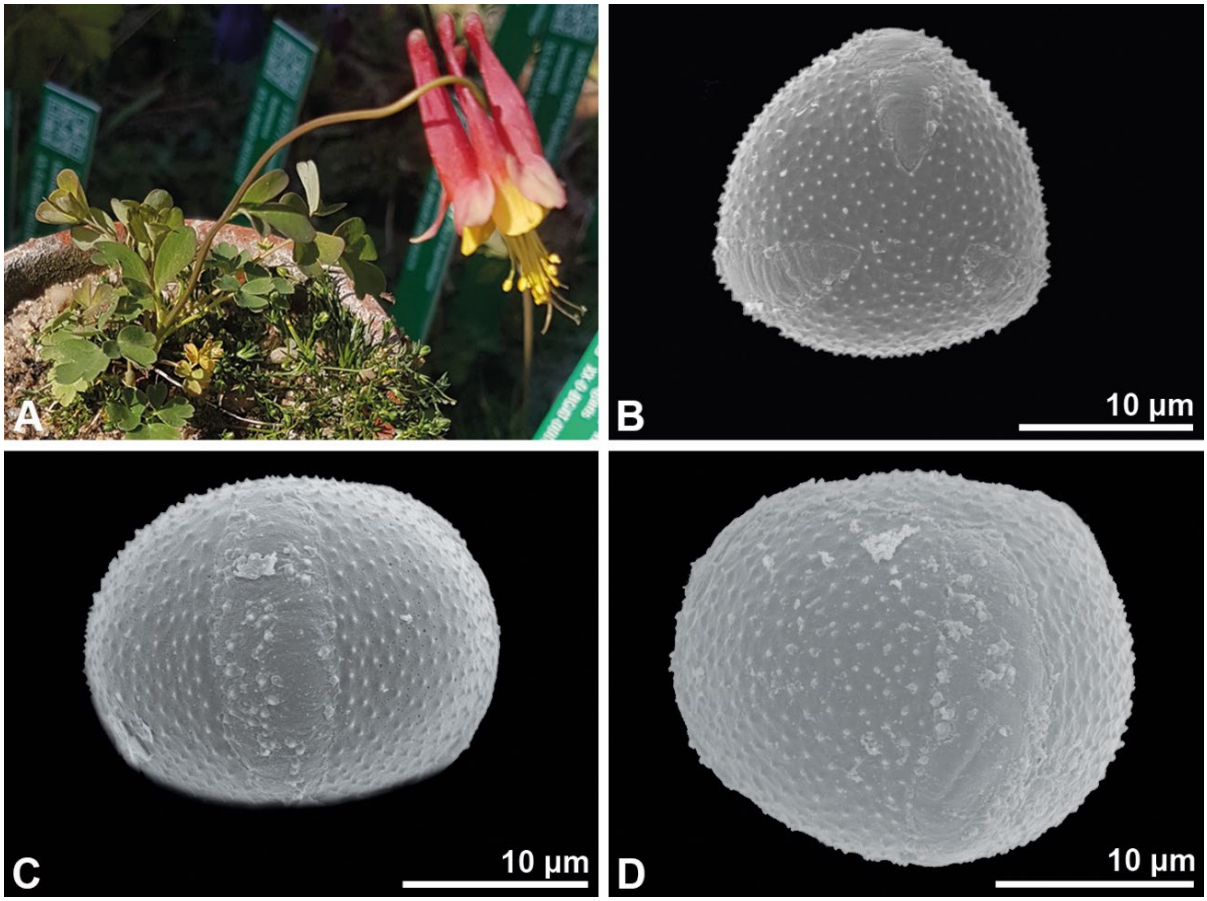

Figure 28: Plant image and scanning electron micrographs of *Aquilegia canadensis* (DMP+CPD)

A. Habitus

B. Hydrated pollen grain in polar view

C-D. Hydrated pollen grain in equatorial view

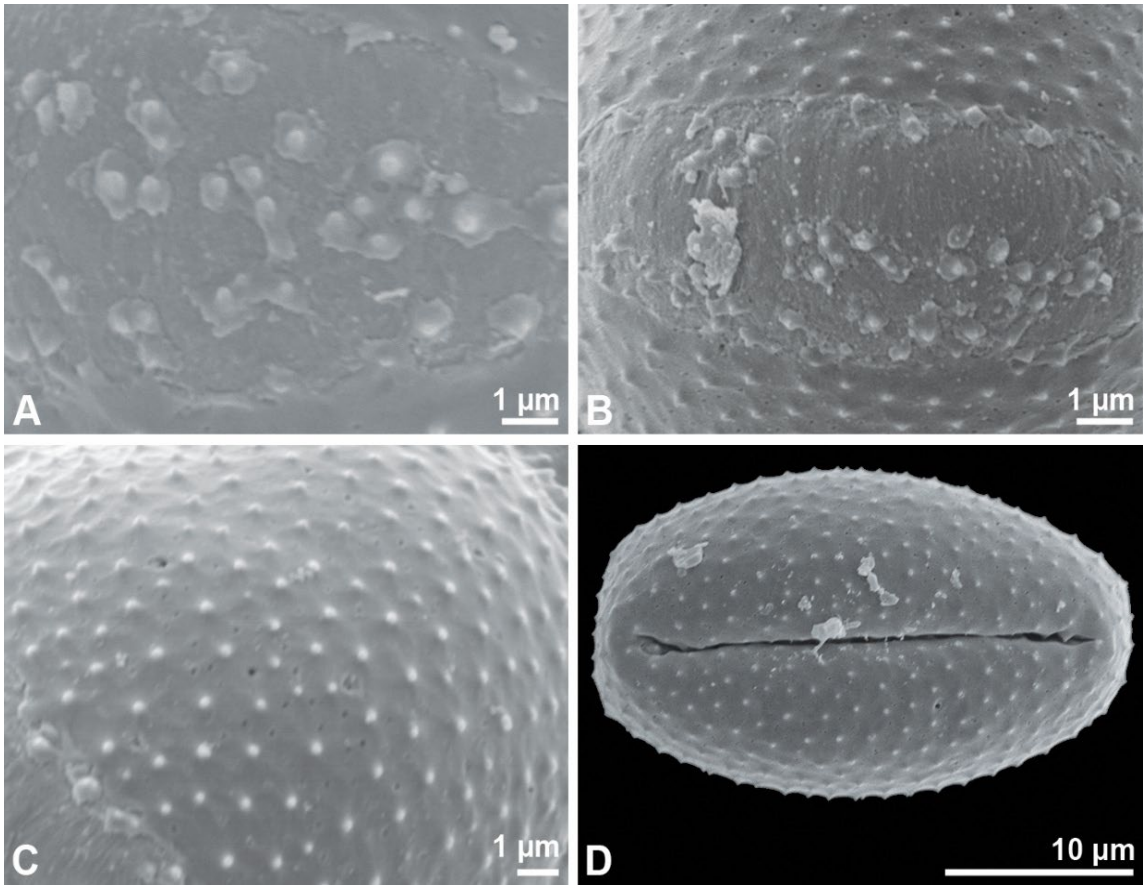

Figure 29: Scanning electron micrographs of *Aquilegia canadensis* (DMP+CPD)

A-B. Detail of aperture

C. Exine surface

D. Dry pollen grain

Pellionia repens (Rosales, Urticaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **small (10-25 µm)**	Shape (Dry Pollen): **irregular**
Pollen Class: **porate**	Outline in Polar View (Dry Pollen): **irregular**
Polarity: **isopolar**	Infoldings (Dry Pollen): **irregularly infolded**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **n/a**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **annulus**
Aperture Condition: **porate, triporate**	Ornamentation SEM: **nanoechinate to microechinate**
Aperture Type: **porus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **present**	

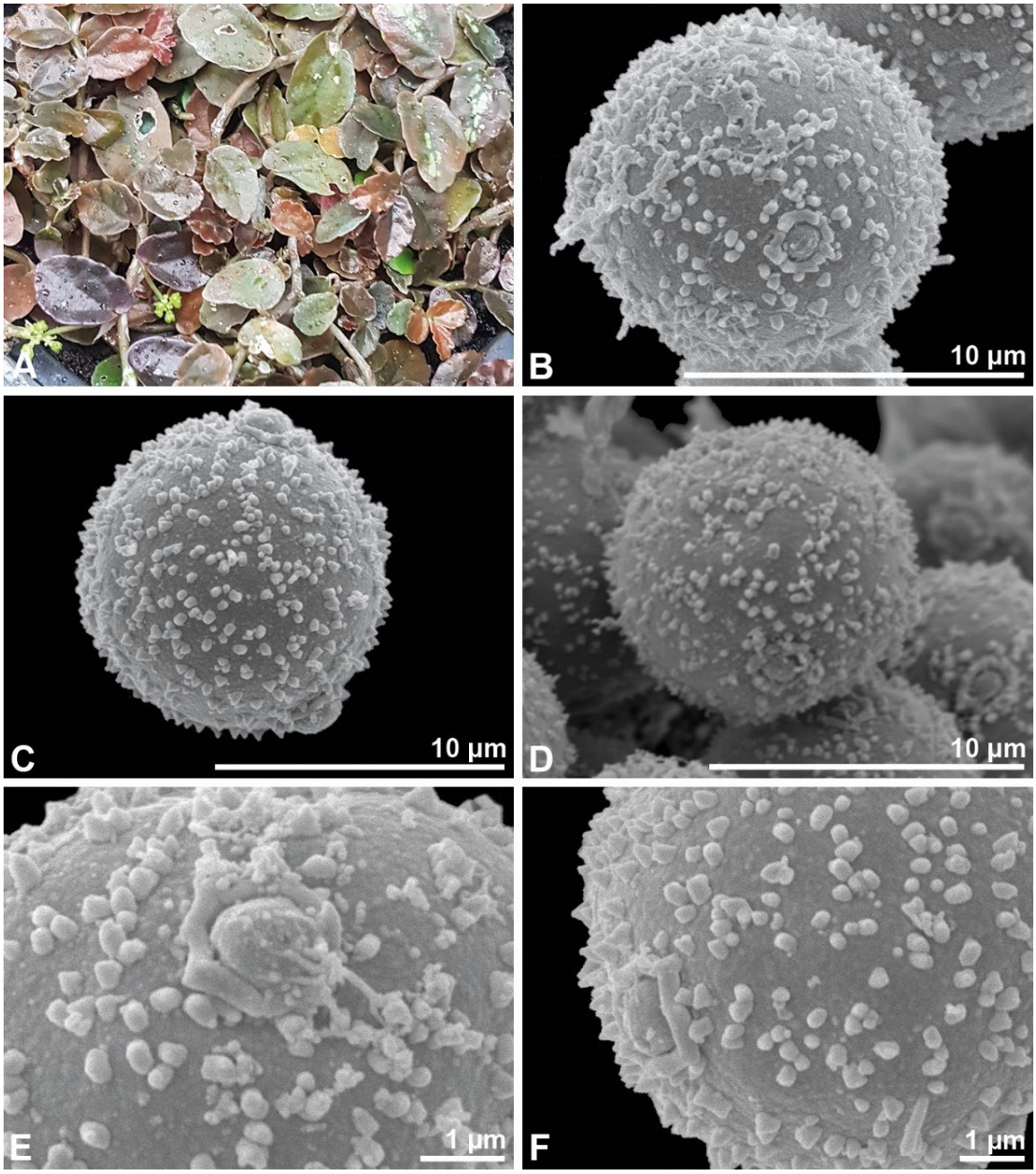

Figure 30: Plant image and scanning electron micrographs of *Pellionia repens* (DMP+CPD)

A. Habitus

B. Hydrated pollen grain in equatorial view

C. Hydrated pollen grain in polar view

D. Hydrated pollen grain in oblique view

E-F. Close-up of aperture and exine surface

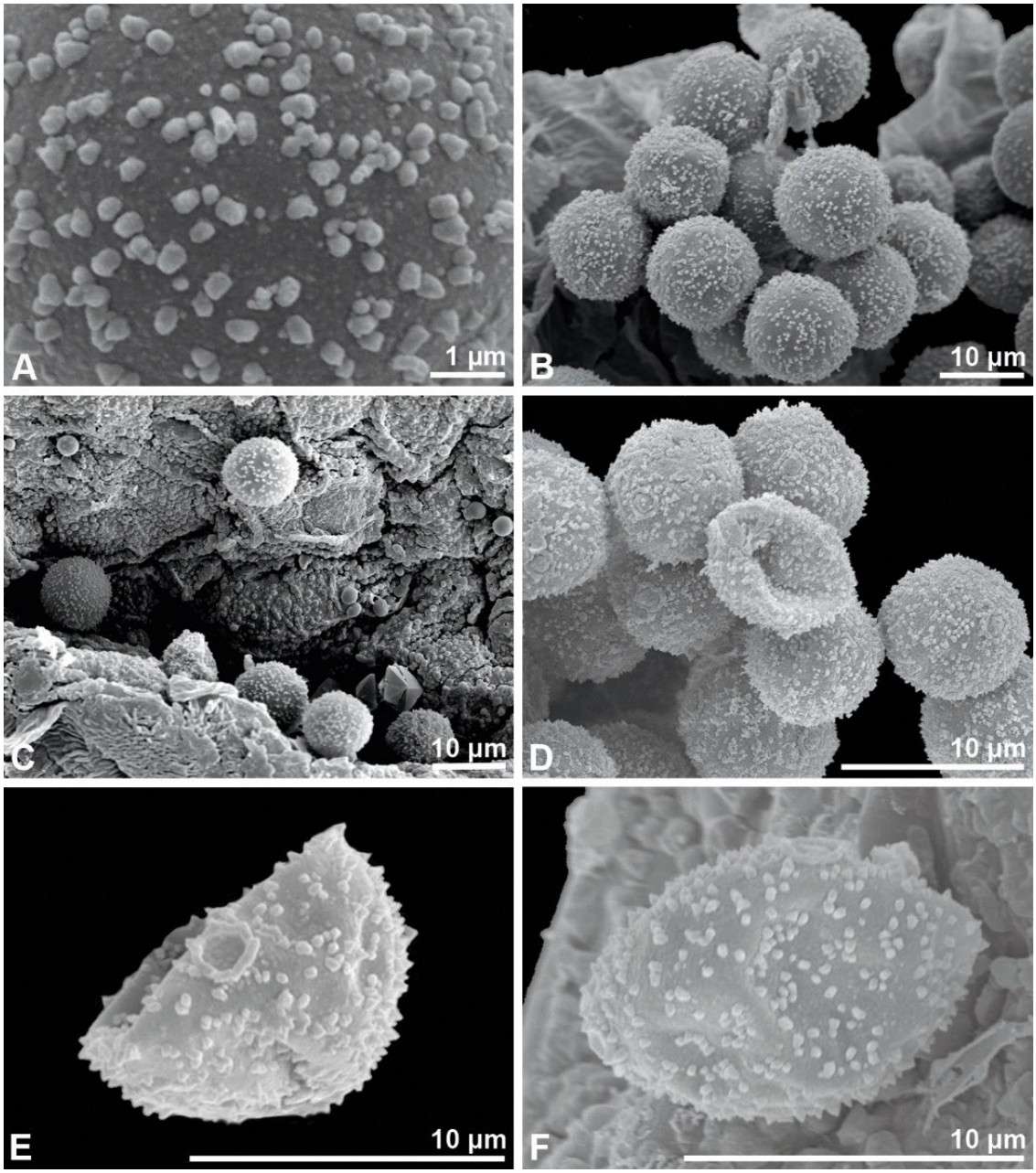

Figure 31: Scanning electron micrographs of *Pellionia repens* (DMP+CPD)

A. Exine surface

B. Hydrated pollen grains in the overview

C. Pollen attached to the inner anther wall, with spherical Ubisch bodies of different size

D. Hydrated and dry (center) pollen grains in the overview

E. Dry pollen grain

F. Dry pollen grain attached to the inner anther wall

Heuchera micrantha (Saxifragales, Saxifragaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **small (10-25 µm)**	Shape (Dry Pollen): **n/a**
Pollen Class: **colporate**	Outline in Polar View (Dry Pollen): **lobate**
Polarity: **isopolar**	Infoldings (Dry Pollen): **aperture(s) sunken**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **prolate**

Aperture and Ornamentation	
Aperture Number: **3**	Aperture Peculiarities: **aperture membrane ornamented**
Aperture Condition: **colporate, tricolporate**	Ornamentation SEM: **microreticulate, microrugulate, perforate**
Aperture Type: **colporus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

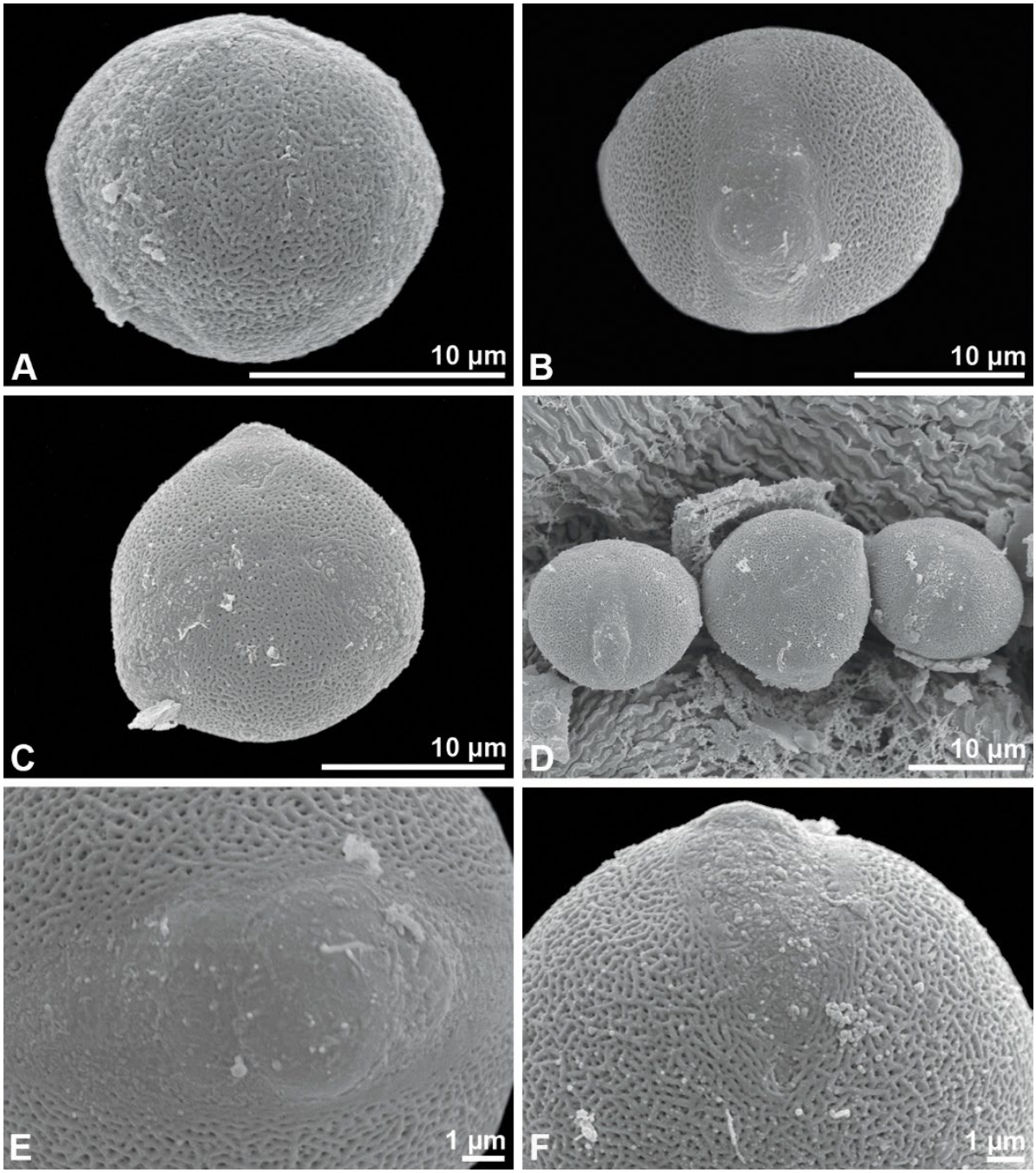

Figure 32: Scanning electron micrographs of *Heuchera micrantha* (DMP+CPD)

A-B. Hydrated pollen grain in equatorial view

C. Hydrated pollen grain in polar view

D. Pollen attached to inner anther wall

E-F. Detail of aperture

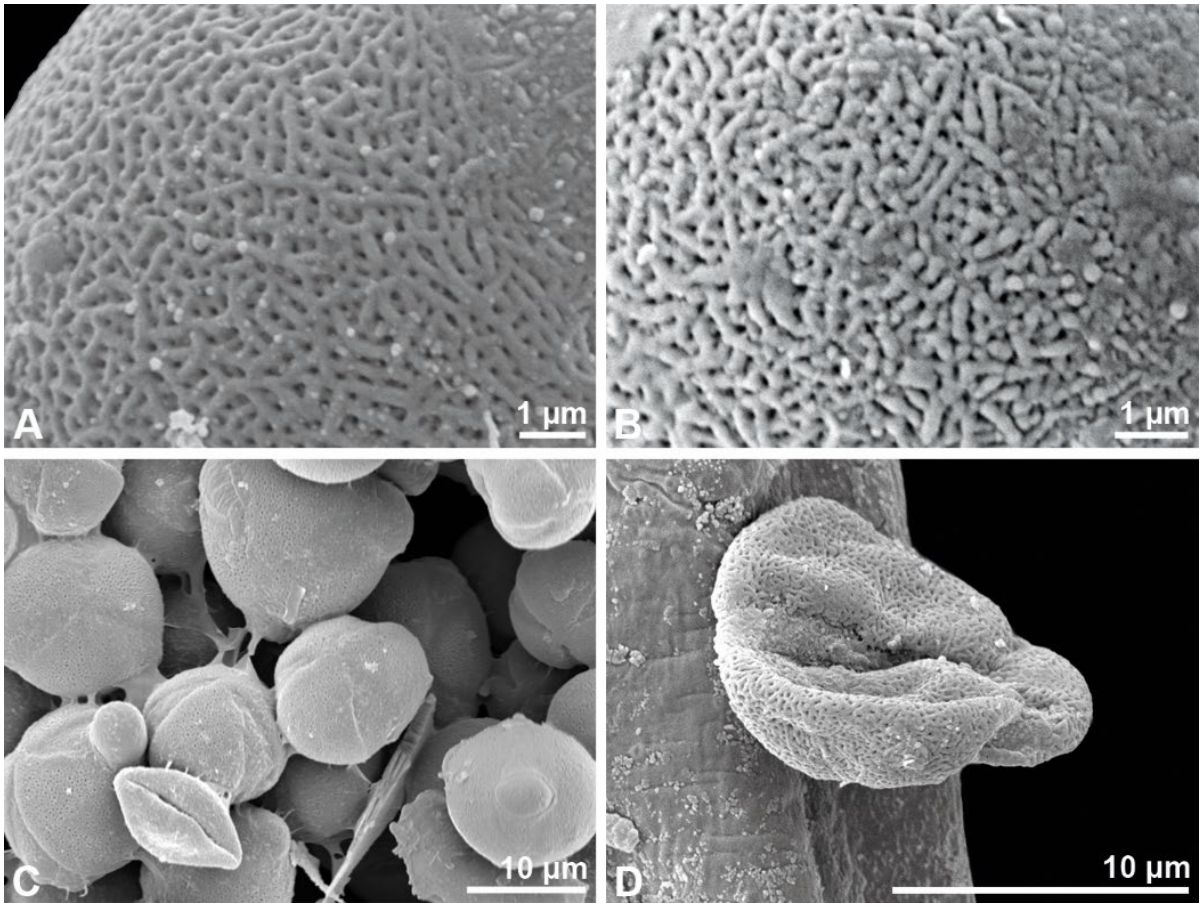

Figure 33: Scanning electron micrographs of *Heuchera micrantha* (DMP+CPD)

A-B. Exine surface

C. Hydrated and dry pollen grains in overview, showing variation in pollen size

D. Dry pollen attached to anther wall

Tribulus terrestris (Zygophyllales, Zygophyllaceae)

Pollen Description

Size and Shape	
Pollen Unit: **monad**	Shape (Hydrated Pollen): **spheroidal**
Dispersal Unit and Peculiarities: **monad**	Outline in Polar View: **circular**
Size (Pollen Unit): **medium-sized (26-50µm)**	Shape (Dry Pollen): **cup-shaped**
Pollen Class: **pantoporate**	Outline in Polar View (Dry Pollen): **irregular**
Polarity: **isopolar**	Infoldings (Dry Pollen): **irregularly infolded**
P/E-Ratio (Hydrated Pollen): **isodiametric**	P/E-Ratio (Dry Pollen): **isodiametric**

Aperture and Ornamentation	
Aperture Number: **>6**	Aperture Peculiarities: **pantoaperturate**
Aperture Condition: **pantoporate**	Ornamentation SEM: **reticulate, homobrochate**
Aperture Type: **porus**	

Miscellaneous	
Pollen Coatings: **n/a**	Wall Peculiarities: **n/a**
Ubisch Bodies: **n/a**	

Annotations
Outline of pollen grains in dry condition can be circular to irregular.

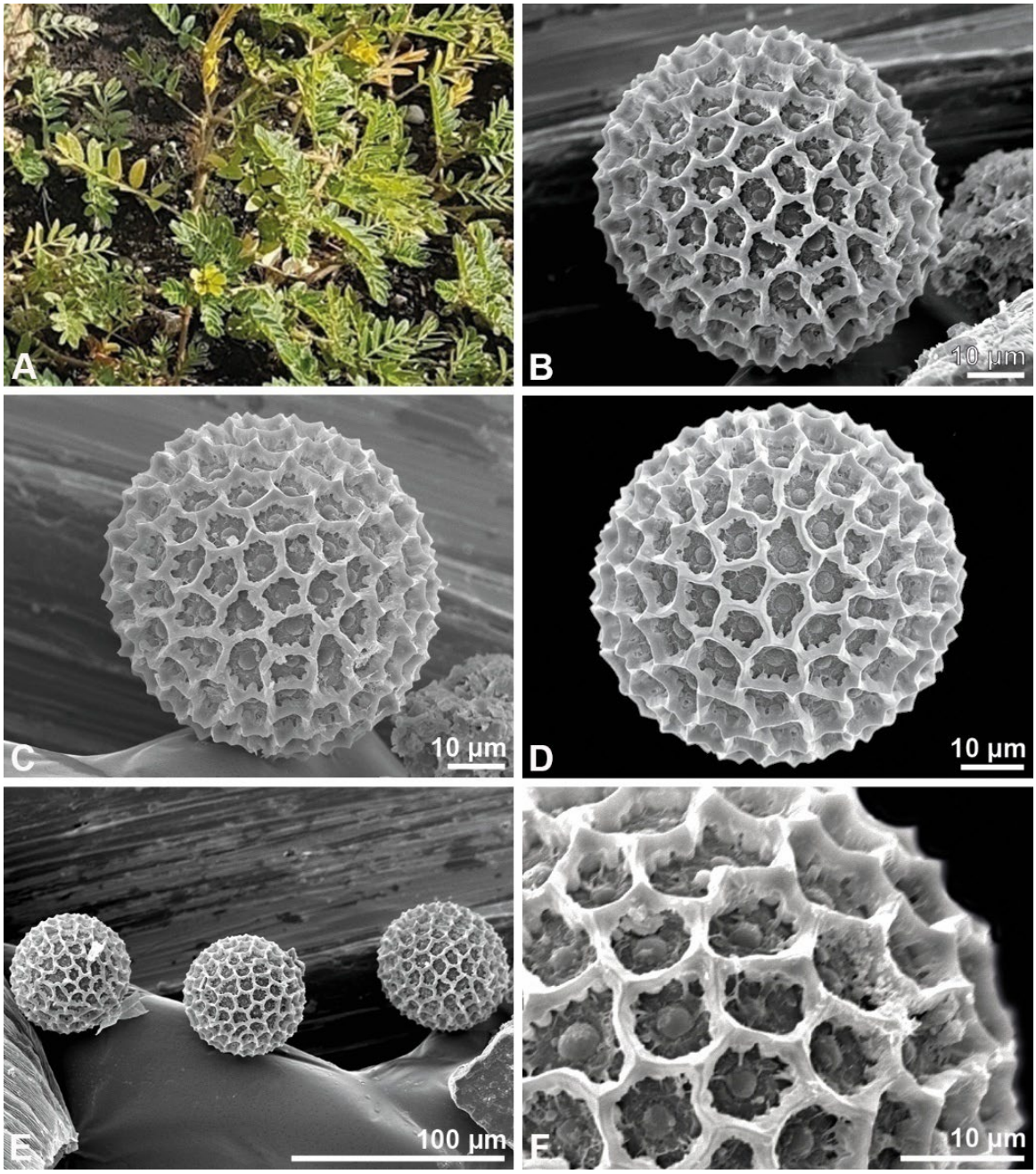

Figure 34: Plant image and scanning electron micrographs of *Tribulus terrestris* (DMP+CPD)

A. Habitus

B-D. Hydrated pollen grains in the overview

E. Overview of hydrated pollen grains on inner anther wall

F. Close-up showing the apertures and exine surface

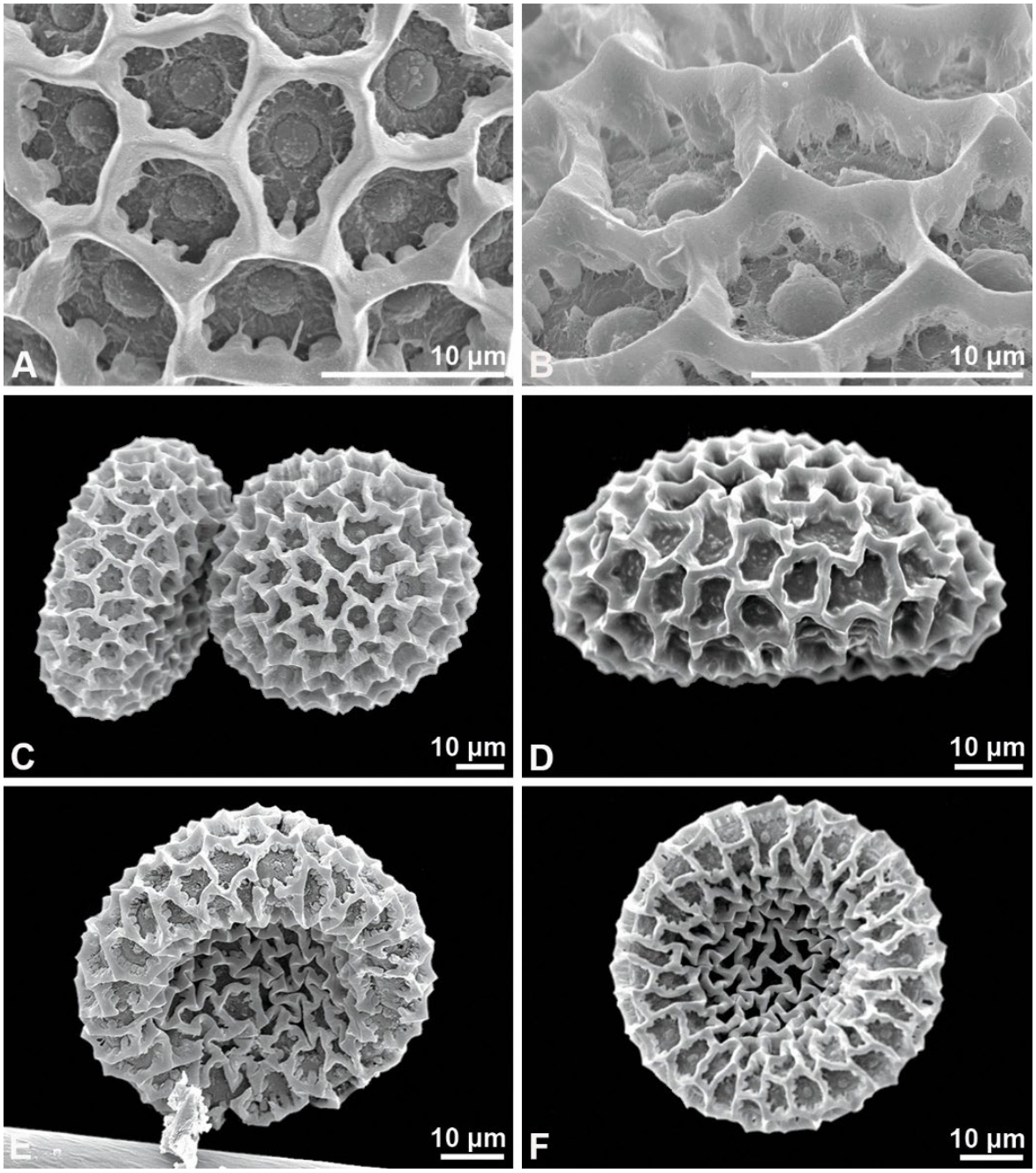

Figure 35: Scanning electron micrographs of *Tribulus terrestris* (DMP+CPD)

A-B. Apertures and exine surface

C. Dry (left) and semi-hydrated (right) pollen

D-F. Dry pollen cup-shaped

Table 3: Summary of the most relevant pollen characters of the investigated species (alphabetically sorted by order)

Taxon	Pollen Unit, Size, and Polarity		Aperture			Ornamentation		Hydrated Pollen			Dry Pollen				Miscellaneous	
Species name	**Size**	**Polarity**	**Number**	**Condition**	**Peculiarities**	**Ornamentation (SEM)**	**Supra-sculpture (SEM)**	**Shape**	**Outline in Polar View**	**P/E-Ratio**	**Shape**	**Outline in Polar View**	**P/E-Ratio**	**Infoldings (dry)**	**Pollen coatings**	**Ubisch bodies**
Acorus calamus [3]	small	heteropolar	1	sulcate	membrane ornamented	perforate, psilate	n/a	spheroidal	elliptic	oblate	cup-shaped	elliptic	oblate	aperture(s) sunken	n/a	present
Spathiphyllum wallisii	small	isopolar	none	inaperturate	n/a	plicate	n/a	spheroidal to elliptical	elliptic	oblate	n/a	elliptic	oblate	n/a	n/a	n/a
Agapanthus africanus	medium	heteropolar	1	sulcate	membrane psilate	microreticulate, heterobrochate	n/a	elliptical	elliptic	oblate	boat-shaped	elliptic	oblate	aperture(s) sunken	n/a	present
Albuca bracteata	very large	heteropolar	1	sulcate	membrane psilate	microreticulate, perforate	n/a	elliptical	elliptic	oblate	boat-shaped	n/a	oblate	aperture(s) sunken	n/a	n/a
Iris missouriensis	large	heteropolar	1	sulcate	membrane psilate	reticulate, free-standing columellae, heterobrochate	n/a	spheroidal to elliptical	elliptic	oblate	boat-shaped	elliptic	oblate	aperture(s) sunken	n/a	present
Reseda alba	small	isopolar	3	colporate, tricolporate	membrane psilate	reticulate	n/a	spheroidal	circular	isodiametric	n/a	lobate	oblate	aperture(s) sunken	n/a	n/a
Rivina humilis	medium	n/a	>6	pantocolpate	membrane psilate	psilate, perforate, foveolate, microechinate	n/a	spheroidal	circular	isodiametric	n/a	irregular	n/a	irregularly infolded	n/a	n/a
Telephium imperati	large	isopolar	3	colpate, tricolpate	membrane ornamented	perforate, nanoechinate	n/a	spheroidal	circular	isodiametric	n/a	lobate	prolate	aperture(s) sunken	n/a	present
Tradescantia spathacea	medium	heteropolar	1	sulcate	membrane ornamented	microverrucate, perforate	n/a	elliptical	elliptic	oblate	boat-shaped	n/a	oblate	aperture(s) sunken	n/a	n/a
Geranium sanguineum	large	isopolar	3	tricolporate	brevicolporus	reticulate, clavate	clavate	spheroidal	circular	isodiametric	irregular	irregular	n/a	irregularly infolded	present	n/a
Jacaranda mimosifolia	medium	isopolar	3	colporate, tricolporate	membrane ornamented	perforate, psilate	n/a	spheroidal	circular	oblate	n/a	lobate	prolate	aperture(s) sunken	n/a	present
Perilla frutescens	medium	isopolar	6	hexacolpate, stephano-aperturate	membrane ornamented	reticulate, bireticulate	n/a	n/a	elliptic	oblate	disc-shaped	elliptic	prolate	aperture(s) sunken	n/a	n/a
Dalechampia spathulata	medium	isopolar	3	tricolporate	brevicolpus	reticulate, free-standing collumelae, heterobrochate	n/a	spheroidal	circular	isodiametric	n/a	lobate	prolate	aperture(s) infolded	n/a	n/a
Aquilegia canadensis	medium	isopolar	3	colpate, tricolpate	membrane ornamented	perforate, nanoechinate	n/a	spheroidal	circular	oblate	n/a	lobate	prolate	aperture(s) sunken	n/a	n/a
Pellionia repens	small	isopolar	3	porate, triporate	annulus	nanoechinate to microechinate	n/a	spheroidal	circular	isodiametric	irregular	irregular	n/a	irregularly infolded	n/a	present
Heuchera micrantha	small	isopolar	3	colporate, tricolporate	membrane ornamented	microreticulate, microrugulate perforate	n/a	spheroidal	circular	isodiametric	n/a	lobate	prolate	aperture(s) sunken	n/a	n/a
Tribulus terrestris	medium	isopolar	>6	pantoporate	pantoaperturate	homobrochate, reticulate	n/a	spheroidal	circular	isodiametric	cup-shaped	irregular	isodiametric	irregularly infolded	n/a	n/a

[3] Color code: Orange - monocots; Blue - eudicots;

Palynological Observations

The pollen morphology of 17 angiosperm species of 17 different families in 13 different orders (Table 2), observed under SEM, were described and illustrated above (Figures 3-35). The pollen characters have been compared and the results are summarized in table 3. For the investigation of pollen in dry condition, the pollen grains have also been dehydrated and critical point dried (DMP+CPD). This method was meant to clean the pollen surface of the dry pollen grains, but as an unintentional side effect, this preparation method leads to predominantly semi-hydrated and less dry pollen grains in the samples, as the air-dried pollen grains partly hydrated in the DMP liquid.

Monocot taxa investigated

The following six monocot species were investigated: *Acorus calamus, Spathiphyllum wallisii, Agapanthus africanus, Albuca bracteata, Iris missouriensis* and *Tradescantia spathulata*. Pollen of all investigated monocots is dispersed as monads.

Acorus calamus L.[4] (Acorales, Acoraceae, Figs. 3-4) pollen grains are small-sized (mean size 15-20 µm), heteropolar, sulcate with ornamented aperture membrane (Fig. 4A). Hydrated pollen is oblate, spheroidal, with elliptic outline (Fig. 3B-D). In dry conditions, pollen grains are cup-shaped, oblate, with elliptic outline (Fig. 4B-E), and the aperture (sulcus) is infolded (Fig. 3F). The pollen ornamentation is psilate and perforate (Fig. 3E). Nanoverrucate Ubisch bodies are present on the inner anther wall (Fig. 4F).

Spathiphyllum wallisii Regel (Alismatales, Araceae, Figs. 5-6) pollen grains are small-sized (mean size 20-25 µm), isopolar, and inaperturate (Fig. 5B-F). Hydrated pollen is oblate, spheroidal to elliptic, with elliptic outline (Fig. 6A-B). In dry conditions, pollen grains are oblate and elliptic (Fig. 6E-F). The pollen ornamentation is plicate (Fig. 6C-D).

Agapanthus africanus Hoffmanns. (Asparagales, Amaryllidaceae, Figs. 7-8) pollen grains are medium-sized (mean size 45-50 µm), heteropolar, and sulcate with psilate aperture membrane (Fig. 8B). Hydrated pollen is oblate, with elliptic shape, and elliptic outline (Fig. 7B-F). In dry conditions, pollen grains are boat-shaped, oblate, elliptic, and the aperture is sunken (Fig. 8D-F). The pollen ornamentation is microreticulate and heterobrochate (Fig. 8C). Spheroidal (globular) Ubisch bodies are present on the inner anther wall (Fig. 8F).

[4] source for the nomenclatural authors - https://tropicos.org/home

Albuca bracteata (Thunb.) J. C. Manning & Goldblatt (Asparagales, Asparagaceae, Figs. 9-10) pollen grains are very large (mean size 105-110 µm), heteropolar, and sulcate, with psilate aperture membrane (Fig. 10A). Hydrated pollen is oblate, with elliptic shape, and elliptic outline (Fig. 9B-F). In dry conditions, pollen grains are boat-shaped, oblate, and the aperture is sunken (Fig. 10E-F). The pollen ornamentation is microreticulate and perforate (Fig. 10C-D).

Iris missouriensis Nutt. (Asparagales, Iridaceae, Figs. 11-12) pollen grains are large-sized (mean size 90-95 µm), heteropolar, sulcate, with psilate aperture membrane. Hydrated pollen is oblate, spheroidal to elliptic, with elliptic outline (Fig. 11A-D). In dry conditions, pollen grains are boat-shaped, oblate, with a sunken aperture (Fig. 12C-D). The ornamentation is reticulate, heterobrochate, with free-standing columellae (Fig. 11E-F; Fig. 12A-B). Spheroidal (globular) Ubisch bodies are present on the inner anther wall (Fig. 12C).

Tradescantia spathulata Sw. (Commelinales, Commelinaceae, Figs. 19-20) pollen grains are medium-sized (mean size 30-35 µm), heteropolar, and sulcate, with ornamented aperture membrane (Fig.19 D-F). Hydrated pollen is oblate, elliptic, with elliptic outline (Fig.19 B-C; Fig.20 A-C). In dry conditions, pollen grains are boat-shaped, oblate, and the aperture is sunken (Fig. 20D-E). The ornamentation is microverrucate and perforate (Fig. 19E).

Eudicot taxa investigated

The following eleven eudicot species were investigated: *Reseda alba, Geranium sanguineum, Dalechampia spathulata, Pellionia repens, Tribulus terrestris, Heuchera micrantha, Aquilegia canadensis, Jaracanda mimosifolia, Perilla frutescens, Rivina humilis* and *Telephium imperati*. Pollen of all investigated eudicots is dispersed as monads.

Reseda alba L. (Brassicales, Resedaceae, Figs. 13-14) pollen grains are small-sized (mean size 20-25 µm), isopolar, tricolporate with psilate aperture membrane (Fig. 14A-B). The colpi are long with distinct margin. The pori are visible only in dry conditions (Fig. 14F). In hydrated condition, pollen can therefore be misinterpreted as colpate. Hydrated pollen is isodiametric, spheroidal with a circular outline (Fig. 13B-F). In dry conditions, pollen grains are lobate, oblate and the aperture is sunken (Fig. 14E-F). The pollen ornamentation is reticulate (Fig. 14C-D).

Geranium sanguineum L. (Geraniales, Geraniaceae, Figs. 21-22) pollen grains are large-sized (mean size 80-85 µm), isopolar, tricolporate, brevicolporate, with psilate aperture

membrane (Fig. 22A-C). Hydrated pollen is isodiametric, spheroidal, with a circular outline (Fig. 21B-E). In dry condition, pollen is irregularly infolded, with irregular outline (Fig. 22F). The pollen ornamentation is reticulate, clavate (Fig. 22D-E), with clavate suprasculpture.

Dalechampia spathulata (Scheidw.) Baill. (Malpighiales, Euphorbiaceae, Figs. 26-27) pollen grains are medium-sized (mean size 45-50 µm), isopolar, tricolporate and brevicolpate, with psilate aperture membrane (Fig. 27A-B). Hydrated pollen is isodiametric, spheroidal, with a circular outline (Fig. 26B-D). In dry conditions, pollen grains are lobate, prolate, and the apertures are irregularly infolded. The pollen ornamentation is reticulate, heterobrochate, with free-standing columellae (Fig. 26E-F).

Pellionia repens (Lour.) Merr. (Rosales, Urticaceae, Figs. 30-31) pollen grains are small-sized (mean size 10-12 µm), isopolar, triporate, annulate, with a psilate aperture membrane (Fig. 30E-F). Hydrated pollen is isodiametric, spheroidal, with a circular outline (Figs. 30B-D; 31B-D). In dry conditions, pollen grains are irregular shaped, with irregular outline, and pollen is irregularly infolded (Fig. 31D-F). The pollen ornamentation is nanoechinate to microechinate (Fig. 31A). Spherical Ubisch bodies of different sizes are present on the inner anther wall (Fig. 31C).

Tribulus terrestris L. (Zygophyllales, Zygophyllaceae, Figs. 34-35) pollen grains are medium-sized (mean size 40-45 µm), isopolar, pantoporate, with psilate aperture membrane (Figs. 34F; 35A-B), and pollen ornamentation is reticulate-homobrochate (Figs. 34F; 35A-B). Hydrated pollen is isodiametric, spheroidal, with a circular outline (Fig. 34B-E). In dry conditions, pollen grains are cup-shaped or irregular shaped, with circular to irregular outlines, and the apertures are infolded (Fig. 35C-F).

Heuchera micrantha Douglas ex. Lindl. (Saxifragales, Saxifragaceae, Figs. 32-33) pollen grains are small-sized (mean size 15-20 µm), isopolar, tricolporate, with ornamented aperture membrane (Fig. 32E-F). Hydrated pollen is isodiametric, spheroidal, with a circular outline (Figs. 32A-D; 33C). In dry conditions, pollen grains are lobate, prolate, and the apertures are infolded (Fig. 33D). The pollen ornamentation is microreticulate, microrugulate and perforate (Fig. 33A-B).

Aquilegia canadensis L. (Ranunculales, Ranunculaceae, Figs. 28-29) pollen grains are medium-sized (mean size 40-45 µm), isopolar, tricolpate, with ornamented aperture membrane (Fig. 29A-B). Hydrated pollen is oblate, spheroidal, with a circular outline (Fig. 28B-D). In dry conditions, pollen grains are lobate, prolate, and the apertures are infolded (Fig. 29D). The pollen ornamentation is perforate and nanoechinate (Fig. 29C).

Jacaranda mimosifolia D. Don (Lamiales, Bignoniaceae, Figs. 23-24) pollen grains are medium-sized (mean size 45-50 µm), isopolar, tricolporate, with ornamented aperture membrane (Fig. 24A). Hydrated pollen is oblate, spheroidal, with a circular outline (Fig. 24B-D). In dry conditions, pollen grains are lobate, prolate, and the apertures are sunken (Fig. 24D). The pollen ornamentation is perforate and psilate (Fig. 24B). Nanoverrucate Ubisch bodies are present on the inner anther wall (Fig. 24C).

Perilla frutescens (L.) Britton (Lamiales, Lamiaceae, Fig. 25) pollen grains are medium-sized (mean size 45-50 µm), isopolar, stephano-hexacolpate, with ornamented aperture membrane (Fig. 25D). Hydrated pollen is oblate, with elliptic outline (Fig. 25B-C). In dry conditions, pollen grains are disc-shaped, elliptic, prolate, and the apertures are infolded (Fig. 25F). The pollen ornamentation is reticulate and bireticulate (Fig. 25E).

Rivina humilis L. (Caryophyllales, Petiveriaceae, Figs. 15-16) pollen grains are medium-sized (mean size 35-40 µm), pantocolpate with more than six apertures, and psilate aperture membrane (Fig. 15C-D). Hydrated pollen is spheroidal, with a circular outline (Figs. 15A-B, E-F; 16C). In dry conditions, pollen grains are irregular in shape and irregularly infolded (Fig. 16E-F). The pollen ornamentation is psilate, perforate, foveolate, and microechinate (Fig. 16A-B). Hydrated pollen grains are often covered by remnants of the tapetum/locular fluid, and the microechini are therefore only clearly visible on dry pollen grains.

Telephium imperati L. (Caryophyllales, Caryophyllaceae, Figs. 18-19) pollen grains are large-sized (mean size 80-85 µm), isopolar, colpate, with psilate aperture membrane (Fig. 18C-D). Hydrated pollen is isodiametric, spheroidal, with a circular outline (Fig. 17B-F). In dry conditions, pollen grains are prolate, with a lobate outline, and the apertures are sunken (Figs. 17D; 18F). The ornamentation is perforate and nanoechinate (Fig. 18A-B). Ubisch bodies are present on the inner anther wall (Fig. 18E), and areolate-nanoechinate shape.

Discussion

Pollen morphology is proven to be a significant tool for modern taxonomy (e.g., Blackmore, 2006; Azzazy, 2016; Gonzaga et al., 2019). The pollen diversity in size, shape, symmetry, polarity, aperture condition, exine ornamentation, and other relevant characters is used to clarify taxonomic relationships (e.g., Furness & Rudall, 2001; Stephen, 2014; Gonzaga et al., 2019). Among the 17 species studied in the present pollen morphological study, six monocot and eleven eudicot taxa were investigated.

Pollen morphology of the investigated monocot species with special regard to its taxonomic relevance

Pollen morphology of the investigated alismatids (monocots).—The alismatids are a group of early diverging monocots, consisting of two orders, Acorales and Alismatales (Stevens, 2001 onwards). The aperture condition of the investigated monocot species is sulcate or inaperturate. A sulcate aperture type is most common in monocots and „is widely considered plesiomorphic in the monocotyledons and early diverging angiosperms "(Oybak Dönmez & Işik, 2008). In many monocot groups, the aperture is reduced to a sulcus-derived aperture (e.g., porus), or pollen grains without defined aperture (inaperturate) occur e.g. in some taxa of the families Araceae, Alismataceae, Chloranthaceae, Liliaceae, Trimeniaceae (Zavada, 1983; Furness & Rudall, 2004; Nadot et al., 2006; Bose et al., 2012). The pollen ornamentation of the investigated species shows many variations, ranging from reticulate, foveolate, psilate, perforate to plicate.

The studied species ***Spathiphyllum wallisii*** belongs to the order Alismatales, family Araceae and subfamily Monsteroideae (Grayum, 1990; Stevens, 2001 onwards). The subfamily Monsteroideae is the third richest clade within the Araceae, with two tribes (Heteropsideae and Spathiphylleae), 11 genera, 385 described species, and about 700 estimated species (Stevens, 2001 onwards; Zuluaga et al., 2015). Within the family of Araceae, the Monsteroideae clade is one of the earliest diverging lineages. They are taxonomically still challenging, and have been included in numerous systematic studies, also including other characters such as e.g., general morphology (e.g., Grayum, 1992) or anatomy (Zuluaga et al., 2015). The genus *Spathiphyllum* comprises about 41 species and belongs to the tribe Spathiphylleae, together with the monotypic genus *Holochlamys* (Friis et al., 2004). Pollen grains of both genera are small to medium-sized, inaperturate, and with plicate to striate exine ornamentation (Friis et al., 2004; Hesse & Zetter, 2007; Tekleva & Krassilov, 2009). Within the Araceae, inaperturate, striate, or plicate pollen

occurs in two subfamilies only, the early diverging Monsteroideae and the derived Aroideae (Mayo et al., 1997; Friis et al., 2004). Pollen of the investigated species *Spathiphyllum wallisii* is inaperturate, with plicate exine ornamentation. According to literature, pollen of *Spathiphyllum* and other Spathiphylleae is either described as inaperturate, with striate pollen ornamentation (Furness & Rudall, 1999; Friis et al., 2004), or inaperturate, with plicate pollen ornamentation (Grayum, 1992; Weber et al., 1999; Hesse & Zetter, 2007). In the study by Grayum (1992) the thickness of the striae is also used to differentiate the species. The pollen ornamentation can be intermediate between striate and plicate, and might therefore be described differently, and may also be a subjective decision by the palynologist (Halbritter et al., 2018). This problem is also discussed in the study by Hesse and Zetter (2007), where some distinctive *Ephedripites* forms with plicate pollen are very similar to the pollen of *Spathiphyllum* and are therefore often misinterpreted in fossil samples. In the study by Friis et al. (2004) the fossil plant *Mayoa portugallica* from the Early Cretaceous is considered to be closely related to *Spathiphyllum* and *Holochlamys*. The authors stated that the fossil pollen of *Mayoa portugallica* shares the same pollen morphological characters (elliptic, inaperturate, striate), including fossilization potential, which are in combination typical characters of Monsteroideae pollen (Friis et al., 2004). Several authors (Furness & Rudall, 1997, 1999; Weber et al., 1999) concluded that inaperturate pollen is most common in the Araceae, except for a small variety of sulcate pollen. The sulcate aperture condition is characteristic for pollen of the investigated species ***Acorus calamus.*** The monocot genus *Acorus* belongs to the order Acorales, family Acoraceae, and includes two species *A. calamus* and *A. gramineus* (Bogner et al., 2011). The sulcate pollen of *Acorus calamus* is small-sized, monad, elliptic, heteropolar, with psilate and perforate ornamentation, which is in accordance with previous pollen studies of the species *Acorus gramineus* (Grayum, 1987, 1992; Furness & Rudall, 1997; Bogner et al., 2011; Lu et al., 2015). The genus *Acorus* was originally placed within the Araceae family and is now placed in the family Acoraceae, within the order Acorales (Bogner et al., 2011). The families Acoraceae and Araceae share some characters as their inflorescences comprise spadix and spathe, but other features, based on morphology and molecular studies, are clearly separating the Acoraceae from the Araceae (Grayum, 1987; Bogner et al., 2011).

Pollen morphology of the investigated lilioids (monocots). —The three investigated species belong to the order Asparagales, one of five orders within the lilioids (Stevens, 2001 onwards). The Asparagales comprises 14 families (e.g., Amaryllidaceae, Asparagaceae, Iridaceae, Orchidaceae), and contains approximately 36,265 species (Stevens, 2001 onwards). The studied species *Agapanthus africanus*, *Albuca bracteata*

and *Iris missouriensis* belong to three different families within the order Asparagales. Most Asparagales display sulcate or porate pollen grains (Penet et al., 2005; Nadot et al., 2006). Variations are present in e.g., the Hemerocallidaceae with trichotomosulcate pollen, or the Iridaceae with sulcate, disulcate, trichotomosulcate, or inaperturate pollen types (Goldblatt & Le Thomas, 1992; Nadot et al., 2006).

The studied species ***Agapanthus africanus*** belongs to the family Amaryllidaceae and comprises 73 genera and 1,605 accepted species**.** The genus *Agapanthus* is the only genus within the subfamily Agapanthoideae with nine accepted species (Stevens, 2001 onwards; Chase et al., 2009; Singh & Baijnath, 2018; Meerow & Cano, 2019). The pollen of *Agapanthus africanus* is medium-sized, monad, sulcate, and reticulate. As far as known, this pollen type is typical for the genus *Agapanthus* and family Amaryllidaceae *(*Kubitzki, 1998; PalDat, 2000 onwards; Golloshi et al., 2017; Başer et al., 2019).

The species ***Albuca bracteata*** belongs to the family Asparagaceae, subfamily Scilloideae, and tribe Ornithogaleae. The family Asparagaceae includes 153 genera and 2,900 species within seven subfamilies (e.g., Agavoideae, Lomandroideae, Nolinoideae, Scilloideae) (Stevens, 2001 onwards).

The results of the present pollen study of *Albuca bracteata* are in accordance with literature findings (Conrado Lopes et al., 2013; Saha & Jha, 2019). Large sulcate pollen grains, with microreticulate-perforate exine ornamentation, seem to be characteristic for the whole subfamily Scilloideae (Saha & Jha, 2019). *Albuca bracteata* was formerly placed in the genus *Ornithogalum* under the name *Ornithogalum longibracteatum.* A recent molecular study by Manning et al. (2009), that included the analysis of four plastid DNA regions of subfamily Ornithogaloideae, resulted in a revised classification. Based on this study, some species from the genus *Ornithogalum* were transferred to the genus *Albuca* (Manning et al., 2009; http://wcsp.science.kew.org/).

The studied species ***Iris missouriensis*** belongs to the family Iridaceae, which comprises eight subfamilies (e.g., Aristeoideae, Iridoideae, Isophysidoideae, Patersonioideae), 66 accepted genera, and 2,244 species. The genus *Iris* belongs to the subfamily Iridoideae, tribe Irideae, and includes 350 accepted species (Stevens, 2001 onwards; Kandemir et al., 2019).

The results of the present pollen study of *Iris missouriensis* are in accordance with previous studies (Goldblatt & Le Thomas, 1992; Mitic et al., 2013). The large-sized sulcate, reticulate pollen type, is characteristic for the subfamily Iridoideae, as shown in the study by Goldblatt and Le Thomas (1992). In a pollen morphological study by Mitic et al. (2013), the sulcus membrane is reported to be typically smooth in the investigated croatian *Iris* species (except for *I. pseudacorus* and *I. sibirica*), whereas the sulcus membrane of the

Turkish samples is typically ornamented (Pinar & Oybak Dönmez, 2000). Their study revealed at least four pollen types, with taxonomic implications on the subgenera level and to the series level (e.g., *Iris* section *Iris*, series *Elatae* and *Pumilae*). The palynological characters used for delimitation of *Iris* are the shape of dry pollen, shape, outline, and size of hydrated pollen, sulcus size and sulcus membrane, and the exine ornamentation. Moreover, the palynological study provided "new insight into taxonomic and evolutionary trends at the subgeneric and infrasubgeneric levels of the genus *Iris* in the territory of Southern Europe" (Mitic et al., 2013).

To conclude, the pollen grains of three investigated Asparagales species (*Agapanthus africanus, Albuca bracteata* and *Iris missouriensis*) are very similar, with small variations. The characteristic pollen features are: heteropolar, oblate sulcate pollen with a psilate aperture membrane and a clear, and well-defined sulcus border. In hydrated condition, the pollen shape is elliptic (except for *Iris missouriensis* with a spheroidal to elliptic shape), with elliptical outline. The size of pollen grains is relatively large (90-110 µm), except in *Iris missouriensis* which is medium to large-sized (90-95 µm). A microreticulate, heterobrochate exine ornamentation is common in *Albuca bracteata* and *Agapanthus africanus*, while a reticulate, heterobrochate exine surface is typical for the genus *Iris* and the whole family of Iridaceae (Oybak Dönmez & Işik, 2008). Ubisch bodies are found in *Iris missouriensis* and *Agapanthus africanus.* In dry conditions, pollen grains are boat-shaped, which is typical for sulcate pollen grains.

Pollen morphology of the investigated commelinids (monocots). —This clade constitutes a well-supported group (Arecales, Commelinales, Poales, Zingiberales) within the monocots (Stevens, 2001 onwards). The studied species ***Tradescantia spathacea*** belongs to the order Commelinales comprising five families (Commelinaceae, Haemodoraceae, Hanguanaceae, Philydraceae and Pontederiaceae), 68 genera and 812 species (Stevens, 2001 onwards; Zuntini et al., 2021). The Commelinaceae is the largest family in the order Commelinales with 40 genera and approximately 652 accepted species. Pollen of the investigated species *Tradescantia spathacea* is medium-sized, monad, sulcate, with microverrucate-perforate ornamentation, which is in accordance with literature findings (Poole & Hunt, 1980; Halbritter & Buchner, 2016). According to previous studies, Commelinaceae pollen is predominantly sulcate, heteropolar, and shed in monads (e.g., Poole & Hunt, 1980; PalDat, 2000 onwards; Halbritter & Buchner 2016; Salamma et al., 2019). There are some exceptions within the Commelinaceae with triaperturate pollen, as described for the species *Tinantia anomala* and *Zebrina purpusii.* In these cases, pollen is sulcate, with two additional apertures positioned proximally near the apices, which may

be interpreted as two sulci, or two small, elongated apertures (tenuitates) (Poole & Hunt, 1980; Halbritter & Buchner, 2016). Pollen studies of the Commelinaceae are still rare (e.g., Poole & Hunt, 1980; PalDat database, 2000 onwards; Halbritter & Buchner, 2016), but so far, the sulcate, heteropolar pollen condition seems to be the most common character in the family (Salamma et al., 2019).

Pollen morphology of the investigated eudicot species with special regard to its taxonomic relevance

The tricolpate or eudicot clade contains approximately 210,000 accepted species (Christenhusz & Byng, 2016). Members of this clade exhibit pollen grains with three apertures, tricolpate or tricolporate, and their derived forms (Judd & Olmstead, 2004). Eudicots may be divided into early diverging lineages and core eudicots. Early diverging eudicots represent the following orders: Buxales, Proteales, Ranunculales and Trochodendrales. Core eudicots include the clades: Gunnerales, Dilleniales, superrosids and superasterids. Superrosids comprise Saxifragales and rosids (Vitales, malvids and fabids). Superasterids consist of Berberidopsidales, Caryophyllales, Santalales and asterids (Cornales, Ericales, campanulids and lamiids) (Chase et al., 2016).

Pollen morphology of the investigated early diverging eudicots. —The investigated species *Aquilegia canadensis* belongs to the order Ranunculales, family Ranunculaceae and subfamily Thalictroideae. The order Ranunculales belongs to the **early diverging eudicots** and includes seven families (e.g., Berberidaceae, Circaeasteraceae, Ranunculaceae), with 199 genera and 4,510 accepted species (Stevens, 2001 onwards; Wang & Chen, 2007).

Pollen of the investigated species ***Aquilegia canadensis*** is medium-sized, monad, tricolpate, with perforate-nanoechinate ornamentation, which is in accordance with literature findings (Wodehouse, 1936; Perveen & Qaiser, 2006; Nahoojei et al., 2008). *Aquilegia* pollen is usually tricolpate, as typical for many Ranunculaceae, but variations of the aperture number exist, such as e.g., in *Aquilegia vulgaris*, with tetra- and hexacolpate pollen (Wodehouse, 1936). Within the family Ranunculaceae, three pollen types are known: tricolpate, pantocolpate and pantoporate, with a nanoechinate, echinate, striate, or verrucate exine ornamentation (Wodehouse, 1936; Perveen & Qaiser, 2006; Nahoojei et al., 2008). According to the literature, pollen grains of the subfamily Thalictroideae are usually small to medium-sized, spheroidal, tricolpate, and microechinate (Wodehouse, 1936; PalDat database, 2000 onwards). Within the subfamily, pollen of the genus

Thalictrum is the only exception with a pantoporate aperture condition (PalDat, 2000 onwards; Tatlidil et al., 2005).

Pollen morphology of the investigated lamiids (asterids, core eudicots). —Asterids consists of three major clades: Cornales, Ericales and Euasterids. The Euasterids consist of the two clades: Lamiids and campanulids. Two of the largest families within the asterids are Asteraceae and Rubiaceae, amongst other families such as Bignoniaceae, Cornaceae, Ericaceae (Steven, 2001 onwards; Bremer et al., 2004; Chase et al., 2016).

The studied species *Jacaranda mimosifolia* and *Perilla frutescens* belong to the order Lamiales. The Lamiales are worldwide distributed from tropical forests to cold habitats, with approximately 25 families (e.g., Bignoniaceae, Byblidaceae, Calceolariaceae, Lamiaceae), including 1,059 genera and 23,755 species (Stevens, 2001 onwards). The Lamiales are variable regarding their pollen morphology. For example, variations in the aperture condition are ranging from dicolporate, tricolporate, tricolpate, hexacolporate, pantoporate to inaperturate pollen types (Yang et al., 2020). These variations are also displayed by the two studied Lamiales species.

The studied species ***Jacaranda mimosifolia*** belongs to the family Bignoniaceae, tribe Jacarandeae (Steven, 2001 onwards; Ragsac et al., 2019). Pollen of the investigated species *Jacaranda mimosifolia* is medium-sized, monad, tricolporate, isopolar, with perforate-psilate exine ornamentation, which is in accordance with most previous studies (Bove, 1993; PalDat, 2000 onwards; Olmstead et al., 2009; Cordeiro et al., 2020). The only contradicting description of *Jacaranda mimosifolia* pollen is presented in a study by Ugbabe et al. (2013), where the exine ornamentation is described as reticulate, although the pollen pictures in the study clearly show a psilate pollen surface (p.257, pictures D-F). But the presented pictures in the study by Ugbabe et al. (2013) are showing pollen grains of *Jacaranda mimosifolia* in dry condition, and in low magnification only, which may have led to a misinterpretation by the authors.

The investigated species ***Perilla frutescens*** belongs to the family Lamiaceae, subfamily Nepetoideae, and tribe Elsholtzieae. The subfamily Nepetoideae contains three tribes (Elsholtzieae, Mentheae and Ocimeae) 105 genera and 3,675 accepted species. Pollen of the investigated species *Perilla frutescens* is medium-sized, oblate, stephano-hexacolpate, with reticulate to bireticulate exine ornamentation. The slim colpi are reaching both poles. The aperture number of *Perilla* pollen may vary from hexacolpate to rare octocolpate, as described by Hu et al. (2010). According to literature findings (Steven, 2001 onwards; Azzazy, 2016; Li et al., 2017), hexacolpate pollen grains are typical for the

subfamily Nepetoideae, which is in accordance with the research findings in the present thesis.

Pollen morphology of the two studied superasterids (core eudicots).—The order Caryophyllales is now placed sister to the asterid clade and comprises around 6% of the eudicot diversity. The Caryophyllales contains 37 families, 749 genera, and currently 11,620 species (Steven, 2001 onwards). The studied species *Rivina humilis* and *Telephium imperati* belong to two different families within the order Caryophyllales.
Pollen of the Caryophyllales is mostly tricolpate, but pantoporate and pantocolpate pollen are also present, while 6- to 8- colpate pollen is rare (Nowicke, 1994). According to literature (PalDat, 2000 onwards; Halbritter et al., 2018), the pollen types found within the the Caryophyllales are very diverse and the main pollen types found are: 1) pantoporate, microechinate pollen, typical for the families Amaranthaceae and Caryophyllaceae, 2) tricolpate, reticulate pollen typical for the Plumbaginaceae, 3) tricolpate, reticulate and/or (micro-) echinate pollen, typical for the Aizoaceae, Phytolaccaceae and Tamaricaceae, 4) tricolpate to porate and microechinate-perforate pollen, found in the Cactaceae, 5) large, stephanoaperturate (porate), gemmate-clavate tetrads of the Droseraceae, and 6) tricolpate, perforate-microechinate to microgemmate pollen of the Polygonaceae. Some exceptions are found at the family level, such as in the Cactaceae, for example, the pantocolpate, microechinate-perforate pollen of the genus *Echinocereus reichenbachii* (Halbritter & Buchner, 2016), or the pantoporate, gemmate pollen of *Eriosyce subgibbosa* (Heigl, 2021), and the pantoporate, reticulate-lophate pollen of *Opuntia* (PalDat, 2000 onwards). Exceptions are also found within the Caryophyllaceae, as pollen of the genus *Herniaria* is typically poroidate, pantoaperturate, microechinate-perforate (PalDat, 2000 onwards), or pollen of the genus *Spergularia* with tricolpate, microechinate-perforate pollen (PalDat, 2000 onwards).

The studied species ***Rivina humilis*** belongs to the family Petiveriaceae, formerly included as subfamily Rivinoideae in the family Phytolaccaceae. The genus *Rivina* is one of nine genera within the Petiveriaceae (e.g. *Gallesia, Schindleria, Trichostigma*), with about 20 known species (Steven, 2001 onwards). Pollen of the family Petiveriaceae is either tricolpate, such as in the genus *Phytolacca* (Halbritter et al., 2021), or pantocolpate, with more than six short colpi typical for the genus *Trichostigma* (Halbritter & Buchner, 2016). Pollen of the investigated species *Rivina humilis* is medium-sized, pantocolpate with psilate, perforate, foveolate to microechinate exine ornamentation. One of the main pollen characters of *Rivina humilis* is the presence of more than six short colpi, spread over the whole pollen surface (pantocolpate), which is in accordance with previous studies by Ebigwai & Egbe (2017). In their study, the aperture condition was the only character to

distinguish between the two genera *Phytolacca* (3-colpate) and *Rivina* (pantocolpate), both formerly included in the Phytolaccaceae. In a study by Bose et al. (2012), *Rivina humilis* is described as “pentazoniporate" (five pores situated at the equator), which seems to be a result of misinterpretation, as pollen was studied by light microscopy only. In the present study, the aperture condition was also unclear, and the results varied depending on the preparation method used: in hydrated condition *Rivina* pollen was covered by remnants of the tapetum/locular fluid, and therefore the microechini have only been detected on pollen in dry condition. According to Halbritter and Buchner (2016), the pollen of *Trichostigma peruvianum* (Petiveriaceae) is also medium-sized, spheroidal, pantocolpate, with perforate, microrugulate, microgemmate, and microechinate ornamentation. Pollen studies of the genus *Rivina* and the Petiveriaceae are still rare, but as far as known, pantocolpate pollen seems to be a common character for the family Petiveriaceae (Halbritter & Buchner, 2016; Ebigwai & Egbe, 2017).

The studied species ***Telephium imperati*** belongs to the family Caryophyllaceae, subfamily Paronychioideae and tribe Corrigioleae. The Caryophyllaceae comprise three subfamilies (Alsinoideae, Caryophylloideae and Paronychioideae), 101 genera, 2,200 accepted species and 2,625 estimated species (Steven, 2001 onwards; Greenberg & Donoghue, 2011). The two genera within the tribe Corrigioleae, *Telephium* and *Corrigola,* were first placed within the family Molluginaceae, and have been transferred to the Caryophyllaceae, subfamily Paronychioideae, based on molecular studies (Greenberg & Donoghue, 2011). According to Harbaugh et al. (2010), the classification of the family Caryophyllaceae is complicated, due to poorly defined genera and difficulty in the determination of phylogenetically useful morphological characters.

Pollen of the investigated species *Telephium imperati* is large, monad, tricolpate, with perforate and nanoechinate exine ornamentation, which is in accordance with literature findings (Eröz Poyraz & Ataslar, 2010; Greenberg & Donoghue, 2011; Al-Taie & Noor Almousawi, 2018). According to Greenberg and Donoghue (2011), tricolpate pollen is the most common pollen type within the subfamily Paronychioideae. Pollen of the family Molluginaceae is described as typically pantocolpate with perforate, microechinate exine ornamentation (Halbritter, 2016; Halbritter et al., 2018). Regarding the pollen morphology of the investigated species *Telephium imperati*, the pollen characters tricolpate, perforate-nanoechinate are shared with those of the subfamily Paronychioideae. The pollen morphology, therefore, supports the placement of the genus *Telephium* within the Caryophyllaceae, based on the study by Greenberg & Donoghue (2011).

Pollen morphology of the investigated superrosids (core eudicots) .—The studied species ***Heuchera micrantha*** belongs to the order Saxifragales, family Saxifragaceae and tribe Heuchereae. The tribe Heuchereae contains 16 genera (e.g., *Asimitellaria, Heuchera*, *Lithophragma*) and 83 species (Steven, 2001 onwards). The pollen morphology of the family Saxifragaceae shows a considerable variation, mostly in the exine ornamentation and pollen shape (PalDat, 2000 onwards; Perveen & Qaiser, 2009). The (tri)colpate or (tri)colporate pollen grains vary from small to medium-sized, mainly spheroidal, with prolate or oblate P/E-Ratio. The exine ornamentation is ranging from striate, rugulate, perforate, microreticulate, reticulate to microgemmate (PalDat, 2000 onwards; Perveen & Qaiser, 2009; Yifeng et al., 2014).

Pollen of the investigated species *Heuchera micrantha* is small, monad, tricolporate, with microreticulate to microrugulate and perforate exine ornamentation. The results are in accordance with previous studies on Heuchera sanguinea (Halbritter & Auer, 2021). So far, pollen morphological studies about the genus *Heuchera* are still rare, but it seems that isopolar, (tri)colporate, microreticulate to microrugulate pollen is the common pollen type for this genus.

Pollen morphology of the investigated malvids (rosids, core eudicots).—Malvids are a clade within the rosids, comprising several orders such as, e.g., Brassicales, Geraniales, Malvales (Chase et al., 2016). The studied species ***Reseda alba*** belongs to the order Brassicales, family Resedaceae, and tribe Resedeae. The Resedaceae comprise three tribes (Astrocarpeae, Cayluseae and Resedeae), eight genera and 96 accepted species. The tribe Resedeae is divided into two subtribes: Randoninae (monotypic genus *Randonia*) and Resedinae (genera *Ochradenus, Oligomeris* and *Reseda*) (Steven, 2001 onwards; Martín-Bravo et al., 2007). According to several authors (Naggar, 2002; Asgari Nematian & Ranjbar, 2021), the family Resedaceae is considered eurypalynous.

Pollen of the investigated species *Reseda alba* is small, monad, tricolporate, with reticulate exine ornamentation, which is in line with literature findings (Naggar, 2002; Çilden et al., 2021). In the present study, the indistinct pores of *Reseda alba* are visible only in dry conditions. The tricolporate pollen grains are characterized by long, narrow colpi and endopori with indistinct margin, which is in accordance with previous studies (Naggar, 2002; Çilden et al., 2021). As reported by the previously mentioned pollen studies on the Resedaceae, variations in the exine ornamentation are ranging from striate, striate-reticulate, reticulate, microreticulate, rugulate-reticulate, microreticulate foveolate, or perforate. Tricolporate or tricolpate, reticulate pollen grains, are common characters for this eurypalynous family (Naggar, 2002; Çilden et al., 2021; Asgari Nematian & Ranjbar,

2021). According to Naggar (2002), the genus *Reseda* is a heterogeneous taxon, and the species can be delimitated by the type of ornamentation.

The studied species ***Geranium sanguineum*** belongs to the order Geraniales, family Geraniaceae and subfamily Geranieae. The order Geraniales includes only two families (Francoaceae and Geraniaceae). The genus *Geranium* represents one of the most diverse genera within the family with currently 430 species (Steven, 2001 onwards). Several authors reported a eurypalynous nature of the Geraniaceae family, based on its diverse pollen morphology (Stafford & Blackmore, 1991; Shehata, 2008). Concerning the exine ornamentation of the Geraniaceae, four types are present: 1) striate-reticulate (e.g. some *Erodium* species), 2) reticulate-gemmae (e.g. *Geranium dissectum, G. molle, G. trilophum*), or 3) reticulate-clavate (e.g. *Geranium asphodeloides*, *G. pusillum,* and *G. rotundifolium*) and 4) reticulate (e.g., *Monsonia heliotropioides, M. senegalensis*, *Pelargonium grandiflorum*) (PalDat, 2000 onwards; Shehata, 2008; Deniz et al., 2013). The results of the present pollen study of *Geranium sanguineum* are in accordance with previous studies on the genus (Verhoeven & Venter, 1992; Shehata, 2008; Deniz et al., 2013). The investigated species *G. sanguineum* represented the common pollen characters typical for the genus *Geranium*. The reticulate-clavate exine ornamentation is covered with pollenkitt. The presence of pollenkitt is also reported in a study by Weber (1996) for the two species *G. robertianum* and *G. pratense*. Weber (1996) reported a tricolpate aperture condition for these two *Geranium* species, while the aperture condition of the investigated species *G. sanguineum* is tricolporate, with a prominent, porus and an indistinct short colpus. It can be concluded that large, isopolar, tricolporate, or tricolpate pollen with reticulate-clavate exine ornamentation represents the common pollen characters for the genus *Geranium*. Moreover, the variation of the aperture condition in this genus can be used, for delimitation on the species level.

Pollen morphology of the investigated fabids (rosids, core eudicots).—Fabids are a clade within rosids, which include orders such as, e.g., Rosales, Fabales, Malpighiales, Zygophyllales (Chase et al., 2016). The studied species ***Dalechampia spathulata*** belongs to the order Malpighiales, family Euphorbiaceae, subfamily Acalyphoideae, tribe Plukenetieae, and the monogenetic subtribe Dalechampiinae (Steven, 2001 onwards; Nowicke & Takahashi, 2002). The tribe Plukenetieae includes about 18 genera (e.g., *Ditaxis*, *Dalechampia, Omphalea, Platygyna*, *Tragia*) and 350 accepted species (Steven, 2001 onwards; Nowicke & Takahashi, 2002). Pollen of the investigated species *Dalechampia spathulata* is medium-sized, monad, tricolporate, with reticulate-heterobrochate exine ornamentation and free-standing columellae, which is in accordance

with literature findings (Punt, 1962; Takahashi et al., 2000; Nowicke & Takahashi, 2002; de Souza, 2017). According to a study by Nowicke & Takahashi (2002), the genus *Dalechampia* has the largest pollen within the subfamily and two thick characteristic costae (equatorial bands) and should therefore be treated as a monophyletic tribe. The costae are only visible under light microscope, and have therefore not been detected in the present study by using the scanning electron microscope only. Hence, the use of different methods and techniques is highly recommended when investigating pollen grains (Halbritter et al. 2018).

The studied species ***Pellionia repens*** belongs to the order Rosales, family Urticaceae and tribe Elatostemateae. The family Urticaceae comprises 54 genera and 2,625 accepted species (Steven, 2001 onwards; Conn & Hadiah, 2011). Pollen from the investigated species *Pellionia repens* is small, isopolar, triporate, with nanoechinate and microechinate exine ornamentation. The pores are surrounded by a smooth margo. The present results are in accordance with literature findings (Sorsa & Huttunen, 1975; PalDat, 2000 onwards; Salim, 2020). The pollen of the Urticaceae is usually small sized (9-29 µm), monad, isopolar, and porate (two to six pores) to pantoporate (up to 20 pores). The pollen surface is usually covered with regularly placed echini (e.g*., Elatostema, Parietaria, Pellionia, Urtica*), but granulate and verrucate exine ornamentations are also present (e.g., *Forsskaolea, Laportea, Parieteria, Urtica*) (Sorsa & Huttenen, 1975; PalDat, 2000 onwards; Salim, 2020).

The studied species ***Tribulus terrestis*** belongs to the order Zygophylalles, family Zygophyllaceae and the subfamily Tribuloideae. The genus *Tribulus* was formerly included within tribe Tribuleae and was later transferred to a higher rank within the Zygophyllaceae, to the subfamily Tribuloideae, based on anatomic evidence (Khalik, 2012). The subfamily Tribuloideae contains six genera (*Balanites, Kallstroemia, Neoluederitzia, Sisyndite*, *Tribulopis,* and *Tribulus*) and 63 accepted species (Praglowski, 1987; Sheahan & Chase, 2000; Steven, 2001 onwards; Lauterbach et al., 2019). Pollen of the investigated species *Tribulus terrestris* is medium-sized, monad, pantoporate, and with reticulate-homobrochate exine ornamentation, which is in accordance with literature findings (PalDat, 2000 onwards; Perveen & Qaiser, 2006; Semerdjieva et al., 2011; Linn et al., 2020). The pores are situated in the middle of each lumen, which is the space enclosed by the muri of the reticulum (Semerdjieva et al., 2011). According to previous studies, the reticulum type of *Tribulus terrestris* is also described as heterobrochate (Erdtman, 1952; Agababian, 1964; Huang, 1972; Kuprianova & Aleyshina, 1978; Semerdjieva et al., 2011; Linn et al., 2020). Regarding the ornamentation, both interpretations are valid, as some of

the muri (meshes of the reticulum) are of different sizes. Hence, the reticulum might also be described as homobrochate to heterobrochate. In the present study, the majority of the brochi and lumina is equal in size and is therefore described as homobrochate. Based on the present study and the literature findings, the characteristic pollen type for the genus *Tribulus* can be summarized as: pantoporate, reticulate-homobrochate to heterobrochate, with apertures situated in the middle of each lumen of the reticulum (Praglowski, 1987; Perveen & Qaiser, 2006; Semerdjieva et al., 2011).

Terminology

The pollen terminology used for the description of pollen grains in the present thesis follows Halbritter et al. (2018).

Aperture Number	**Number of aperture(s) per pollen grain**
1, 2, 3....	The number of apertures is indicated by the prefixes: mono-, di-, tri-, tetra-, penta-, hexa-, and poly-.
no aperture	Pollen grain without aperture(s)

Aperture Type	**Describes the aperture with respect to shape (elongated, round), structure (simple or compound apertures), and location (equatorial, polar, global)**
colpus	Elongated aperture (length/width ratio >2) situated at the equator or globally distributed
colporus	Compound aperture composed of a colpus (ektoaperture) combined with an endoaperture of variable size and shape
no aperture	Pollen grain without aperture
sulcus	Elongated aperture located distally
porus	Circular aperture located at the equator or spread over the pollen grain

Aperture Condition	**Describes the aperture type and/or aperture number of a pollen grain, with respect to location (polar, equatorial, global)**
colpate	Pollen grain with colpi
inaperturate	Pollen grain without distinct apertures
hexacolpate	Pollen grain with six colpi
porate	More or less circular aperture; pori located at the equator or regularly spread over the pollen grain
pantoporate	Pollen grain with pori distributed regularly over the surface

stephanoaperturate	Apertures situated at the equator; Term used for six or more apertures
sulcate	Elongated aperture located distally
tricolpate	Pollen grain with 3 colpi
triporate	Pollen grain with 3 pori

Aperture Peculiarities	**Characteristics of the aperture(s)**
aperture membrane	The exine layer covering an aperture; can be psilate or ornamented
annulus	Ring like wall thickening surrounding a porus or ulcus
brevicolpus	Short colpus situated equatorially; „brevi“– prefix meaning short
pantoaperturate	Pollen grain with apertures distributed more or less regularly over the surface

Dispersal Unit and Peculiarities	**Unit in which pollen is dispersed**
monad	Unit consisting of a single pollen grain

Infoldings (Dry pollen)	**The consequence of harmomegathy in dry condition**
aperture(s) sunken	The characteristic shape of pollen grains in a dry condition as a consequence of harmomegathy
irregularly infolded	Aperture(s) and/or interapertual area(s) sunken

Ornamentation SEM	**The internal structure of the pollen wall**
clava/clavate	Pollen wall with clavae longer and/or wider than 1 µm (clava: club-shaped element)
echinate	Pollen wall with echini longer and/or wider than 1 µm (echinus: pointed ornamentation element)
heterobrochate	Reticulate pollen wall with lumina of different sizes
homobrochate	Reticulate pollen wall with lumina of uniform size

foveolate	Pollen wall with foveolae (roundish lumen more than 1 µm in diameter; distance between two adjacent lumina larger than their diameter)
free standing columellae	Columellae not covered by a tectum in semitectate pollen grains
micro- microechinate microreticulate microverrucate	Prefix for small; features between 0,5 and 1 µm
nano- nanoechinate	Prefix for very small, features between 0.1 and 0.5 µm
reticulate	Pollen wall with reticulum (a network-like pattern consisting of muri and lumina)
bireticulate	Reticulate ornamentation, where the lumina of the coarse-meshed reticulum are filled by a fine-meshed reticulum
perforate	Pollen wall with holes less than 1 µm in diameter
plicate	Pollen wall with plicae (coarse parallel ridges)
psilate	Pollen wall with a smooth surface

Suprasculpture SEM	**Secondary sculpture elements positioned on the primary sculpture of the pollen surface**
clava	Club-shaped element

Outline in Polar View	**Describes the contour of pollen grains in polar and/or equatorial view**
circular	General term, used in palynology describing e.g., „outline“
elliptic	A general term, used in palynology describing e.g., „outline“
boat-shaped	The characteristic shape of sulcate pollen grains in dry condition, as a consequence of harmomegathy

lobate	Outline in a polar view of a pollen grain with bulged interapertural areas
irregular	A general term, used in palynology describing e.g., „outline“, „shape“
Pollen Shape	**3-dimensional form of a pollen grain in relation to the P/E-Ratio**
spheroidal	A general term, used in palynology describing e.g., „shape“
irregular	A general term, used in palynology describing e.g., „outline“, „shape“
cup-shaped	The characteristic shape of pollen grains in dry condition, as a consequence of harmomegathy
boat-shaped	The characteristic shape of sulcate pollen grains in dry condition, as a consequence of harmomegathy

Pollen Size	**Size of pollen Unit: Mostly varies from 10 µm to 100 µm, although smaller and larger types exist. The size depends also on the degree of hydration and the preparation method.**
Size categories	Recommended size categories are: very small (<10 µm), small (10 – 25 µm), medium (26 – 50 µm), large (51 – 100 µm) and very large (>100 µm).

Polarity	**Orientation of the proximal and distal pole of a pollen grain resulting from tetrad stage**
isopolar	Pollen grain with identical proximal and distal faces
heteropolar	Pollen grain with different proximal and distal faces

Pollen Class	**Artificial grouping of pollen grains that share one or more distinctive characters**
colpate	Pollen grain with colpi
colporate	Pollen grain with colpori

inaperturate	Pollen grain without distinct aperture
sulcate	Pollen grain with a sulcus
pentaporate	Pollen grain with five apertures
plicate	Pollen wall with plicae
porate	Pollen grain with pori

P/E-Ratio	**Length of the polar axis between the two poles compared to the equatorial diameter, in hydrated and dry conditions.**
oblate	Pollen grain with a polar axis shorter than the equatorial diameter
prolate	Pollen grain with polar axis longer than the equatorial diameter
isodiametric	Pollen grain with a polar axis equal to the equatorial diameter

Pollen Coatings	**The general term applied to organic compounds usually produced by the tapetum, located on the exine and/or in exine cavities**
pollenkitt	Pollen coating consists of sticky substances, mainly lipids

Wall Peculiarities	**Specific pollen features, characteristic for pollen types/ plant taxa, often related to the pollen wall or the inner anther wall.**
Ubisch bodies	Polymorphic sporopollenin elements produced by the tapetum

Abbreviations

DMP	2,2-dimethoxypropane
CPD	Critical Point Dried
SEM	Scanning Electron Microscope
n/a	not applicable

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