Pollen morphology of the southern African tribe Teedieae, an early-branching lineage of crown Scrophulariaceae

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Pollen morphology of the southern African tribe *Teedieae*, an early-branching lineage of crown *Scrophulariaceae*

Abstract

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The pollen morphology of seven species representing four genera of the tribe *Teedieae* (*Scrophulariaceae*) is described and illustrated using light microscopy (LM) and scanning electron microscopy (SEM). Two major pollen types, 3-colporate and 4-colporate, are recognized by aperture types. Within these pollen types, subtypes are distinguished based on exine sculpture, colpi, colpus membrane, and endoaperture characters. Within type I (3-colporate), three subtypes are recognized: Ia – sculpture psilate, rarely with microperforations; Ib – sculpture microperforate and microreticulate; and Ic – sculpture macroreticulate. Type II (4-colporate) is represented by only one subtype IIa – sculpture psilate, rough, and foveolate. The revealed characteristics of pollen grains are taxonomically significant at the generic and specific levels. Our palynomorphological data are consistent with the results of molecular phylogenetic studies. Pollen grains in *Teedieae* are typically characterized by the colporate aperture type (probably ancestral in *Scrophulariaceae*) and rather primitive characters of surface and sculpture of colpi membranes. Similar palynomorphological patterns in *Teedieae* and *Buddlejeae* can be viewed as ancestral for pollen characters observed in more advanced clades of *Scrophulariaceae.*

Additional key words: exine sculpture, palynomorphology, phylogeny, systematics

Introduction

The tribe *Teedieae*, in its present circumscription, belongs to the family *Scrophulariaceae*, and its placement in this family in the strict sense is confirmed by recent molecular phylogenetic studies (Olmstead & Reeves 1995; Olmstead & al. 2001; Oxelman & al. 2005; Tank & al. 2006). As currently understood, the tribe is a rather compact group represented by (6 or)7(or 8) genera and 14 or 15 species, geographically restricted to S and SW Africa and Madagascar (Fischer 2004; Olmstead 2012). However, this group is important and interesting from a phylogenetic viewpoint, since its members have been revealed to be among the early branching lineages of the large clade containing also the crown clades of *Scrophulariaceae*, corresponding to tribes *Buddlejeae*, *Limoselleae*, and *Scrophularieae* (Oxelman & al. 2005). According to Oxelman & al. (2005), "*Teedieae*, *Buddlejeae*, *Camptoloma*, *Phygelius*, *Manuleeae*, and *Scrophularieae* form a very strongly supported monophyletic group based on chloroplast DNA sequences." In this article we informally refer to this group as "crown *Scrophulariaceae*".

The circumscription of *Teedieae* was rather contradictory, and some taxonomic problems still remain, even after recent molecular studies. Some researchers placed *Oftia* Adans. in the family *Myoporaceae* (Takhtajan 1966; Cronquist 1981; and others), *Spielmaniaceae* (Takhtajan 1987) or even in its own family, *Oftiaceae* (Takhtajan 1997, 2009).

According to molecular phylogenetic studies (Oxelman & al. 2005; Tank & al. 2006), the *Teedieae* include the genera *Dermatobotrys* Bolus, *Freylinia* Colla, *Of-*

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tia, *Teedia* Rudolphi and probably some others, and are strongly supported as a monophyletic group. Takhtajan (2009) included in *Teedieae* only the genera *Ranopisoa* J.-F. Leroy and *Teedia*. He placed *Dermatobotrys* in the tribe *Russelieae*, and separated *Freylinia* and *Phygelius* E. Mey. ex Benth. in the tribe *Freylinieae*. According to recent data, the *Freylinieae* (Barringer 1993) probably do not merit recognition and this name should be considered a synonym of *Teedieae*. Barringer (1993) included in his *Freylinieae* the genera *Antherothamnus* N. E. Br., *Freylinia*, *Manuleopsis* Thell. and *Phygelius*; such circumscription has not been supported by molecular phylogenetic studies (Oxelman & al. 2005). Reveal (2012) placed *Buddlejeae* and *Teedieae* in a separate subfamily, *Buddlejoideae*. Further discussion of relationships of and within *Teedieae* is provided by Oxelman & al. (2005).

According to a working version of the synoptical classification of *Lamiales* (Olmstead 2012), the *Teedieae* include *Dermatobotrys*, *Freylinia*, *Manuleopsis*, *Oftia*, *Phygelius*, *Ranopisoa* (probably better placed in *Oftia* s.l.) and *Teedia*. In this system, *Manuleopsis* is also placed in *Limoselleae* (most probably a technical error), and *Antherothamnus* belongs to *Scrophularieae* (which is confirmed by molecular data).

Thus, easily observed morphological characters of the mentioned genera seem to be contradictory or even misleading, allowing various options of placement of these taxa in a phylogenetic system. In view of that, it is advisable to add to the analysis also some additional micromorphological characters, including palynomorphological ones. Our recent studies of pollen morphology of *Scrophulariaceae* and related families of *Lamiales* (Tsymbalyuk & Mosyakin 2009, 2010, 2012, 2013) and comparison of their results with recent molecular phylogenetic data revealed some important trends in pollen character evolution within the group. However, some phylogenetically important groups of *Scrophulariaceae* remained poorly studied palynomorphologically, or not studied at all. It is especially true for some little-known and geographically restricted genera, especially those occupying phylogenetically crucial early-branching positions in available cladograms.

We believe that a better understanding of phylogenetic distribution of pollen morphology patterns in *Teedieae*, a lineage branching between the early-branching ("basal") and crown *Scrophulariaceae*, is therefore important for reconstructing the evolution of pollen character in the group.

The objectives of our research were to identify the main morphological characters of pollen grains in representatives of *Teedieae* and their correlation with molecular phylogenetic data, to assess their taxonomic significance, and to explore possibilities of their use for solving taxonomic problems.

The available information about pollen grains of representatives of *Teedieae* is rather scarce. Erdtman (1952) studied pollen grains of *Oftia africana* (L.) Bocq. using light microscopy. Niezgoda & Tomb (1975) studied pollen grains of *Scrophulariaceae* (tribe *Leucophylleae*) and *Myoporaceae* using light, scanning and transmission electron microscopy. They included in their research only one species of *Oftia* (*O. africana*) and reported that this species has 4-colpate pollen grains with foveolate sculpture of the exine. They stated that in these features it differs from other studied representatives of *Scrophulariaceae* and *Myoporaceae*, which usually have 3-colpate-diorate pollen grains and reticulate and rugulate sculpture of the exine (Niezgoda & Tomb 1975). In our opinion, this interpretation is inaccurate, since *O. africana* has 4-colporate pollen grains.

In conclusion, published results of previous palynomorphological investigations reported little information concerning peculiarities of pollen grains in *Teedieae.* Six species, of which pollen morphology is reported here, have never been studied palynologically before.

Material and methods

Pollen from seven species belonging to four genera (*Freylinia*, *Oftia*, *Phygelius*, *Teedia*) of *Teedieae* was sampled in the herbarium of the Missouri Botanical Garden, St Louis, Missouri, U.S.A. (MO).

Pollen morphology was studied using light microscopy (LM) and scanning electron microscopy (SEM). For light microscopy studies (LM, Biolar, ×700), the pollen was acetolysed following Erdtman (1952). For size determinations, 20 measurements were taken along the polar and equatorial axes for each species.

For scanning electron microscopy (SEM, JSM-6060LA), pollen grains were treated with 96 % ethanol, then these samples were sputter-coated with gold at the Center of Electron Microscopy of the M. G. Kholodny Institute of Botany (Kyiv, National Academy of Sciences of Ukraine). The micrographs were minimally edited with Adobe Photoshop 5.5 to enhance the images.

Terminology used in descriptions of pollen grains mainly follows the glossaries by Punt & al. (1994) and Tokarev (2002), with some necessary adjustments.

Results

General description of pollen grains

Pollen grains in monads, radially symmetrical, isopolar, 3-colporate or 4-colporate, oblate-spheroidal, spheroidal, and prolate; mainly medium-sized, occasionally in some taxa small; polar axis (P) 18.6–31.9 μm, equatorial diameter (E) 18.6–31.9 μm. Outline in polar view (amb) 3-lobate, slightly 3-lobate, 4-lobate, or slightly 4-lobate. Colpi of the following types: (1) long, narrow, 1.3–2.7 μm wide, ends acute; (2) long, medium-width, 2.4–4 μm wide, ends rounded; (3) long, wide, 4–5.3 μm wide, ends acute; (4) short, narrow, 1.1–1.6 μm wide,

Table 1. Summary of pollen types and subtypes.

Taxon	Pollen type and subtype	Apertures	Colpi	Endoaperture	Exine sculpture
Freylinia lanceolata	Ia	3-colporate	long, medium-width, ends rounded	circular	psilate, rarely with microperforations
Freylinia tropica	Ib	3-colporate	long, narrow, ends acute	elliptical	microperforate, microreticulate
Phygelius capensis	Ib	3-colporate	long, wide, ends acute	elliptical	microperforate, microreticulate
Phygelius aequalis	Ic	3-colporate	long, wide, ends acute	circular	macroreticulate
Oftia africana	IIa	4-colporate	short, narrow, ends rounded	rectangular	psilate, foveolate
Oftia revoluta	IIa	4-colporate	short, medium-width, ends rounded	rectangular	psilate, rough, foveolate
Teedia lucida	IIa	4-colporate	short, wide, ends rounded	rectangular, square	psilate, rough, foveolate

ends rounded; (5) short, medium-width, 1.6–2.4 µm wide, ends rounded; (6) short, wide, 2–4 µm wide, ends rounded. Colpus membrane with psilate or granulate surface.

Endoapertures distinct or indistinct, 3.3–9.3 µm long, 2.4–9.3 µm wide, of the following types: (1) circular (in *Freylinia lanceolata*, *Phygelius aequalis*), (2) elliptic (*F. tropica*, *P. capensis*), (3) rectangular (*Oftia africana*, *O. revoluta*), (4) rectangular and square (*Teedia lucida*).

Exine thin, 1.1–2 µm thick. Tectum nearly equal to infratectum (columellae layer) or 2× thinner than lower layers. Columellae distinct or indistinct, thick, short, arranged regularly. Exine sculpture psilate, rough, microperforate, foveolate, microreticulate, or macroreticulate.

Pollen types and subtypes

Pollen grains in the studied taxa can be subdivided into two basic types, based on their aperture types. Each type contains one to three subtypes, separated mainly according to the exine sculpture but also partly using details of the colpi and endoapertures (Table 1).

Type I: 3-colporate. This type includes two genera: *Freylinia* and *Phygelius.*

Subtype Ia: Sculpture psilate, rarely with microperforations; colpi long, medium-width, 2.4–4 µm wide, ends rounded; colpus membrane psilate; endoapertures circular: *Freylinia lanceolata*.

Subtype Ib: Sculpture microperforate and microreticulate.

1. Colpi long, narrow, 1.3–2.7 µm wide, ends acute; colpus membrane psilate; endoapertures elliptic: *Freylinia tropica*.

2. Colpi long, wide, 4–5.3 µm wide, ends acute; colpus membrane psilate; endoapertures elliptic: *Phygelius capensis*.

Subtype Ic: Sculpture macroreticulate; colpi long, wide, 4 µm wide, ends acute; colpus membrane psilate; endoapertures circular: *Phygelius aequalis.*

Type II: 4-colporate. This type includes two genera: *Oftia* and *Teedia.*

Subtype IIa: Sculpture psilate, rough, and foveolate.

1. Colpi short, narrow, 1.1–1.6 µm wide, ends rounded; colpus membrane psilate; endoapertures rectangular: *Oftia africana.*

2. Colpi short, medium-width, 1.6–2.4 µm wide, ends rounded; colpus membrane psilate and granulate; endoapertures rectangular: *Oftia revoluta*.

3. Colpi short, wide, 2–4 µm wide, ends rounded; colpus membrane psilate and granulate; endoapertures rectangular or square: *Teedia lucida.*

Descriptions of pollen grains

Freylinia Colla

Freylinia lanceolata (L. f.) G. Don (Fig. 1A–D; 3A–D).

LM — Pollen grains 3-colporate, oblate-spheroidal and occasionally spheroidal. Amb (polar view) slightly 3-lobed. P=23.9–30.6 µm, E=23.9–31.9 µm. Colpi long, 2.4–4 µm wide, with indistinct, ± strict margins, slightly thickening near endoapertures, tapering to rounded ends; colpus membrane psilate. Endoapertures distinct, circular, 5.3–9.3 µm long, 4–9.3 µm wide. Exine 1.1–1.6 µm thick. Exine layers indistinct, sometimes tectum 2× thinner than lower layers. Columellae distinct, thick, short, arranged regularly. Exine sculpture psilate.

SEM — Sculpture psilate, rarely with microperforations.

Specimen investigated — South Africa: Western Cape province: S Cape (Quarter degree Grid Ref. 3321 AD, Ladismith), Sevenweekspoort, streamsides, 14 Mar 1981, *L. Hugo 2576* (MO).

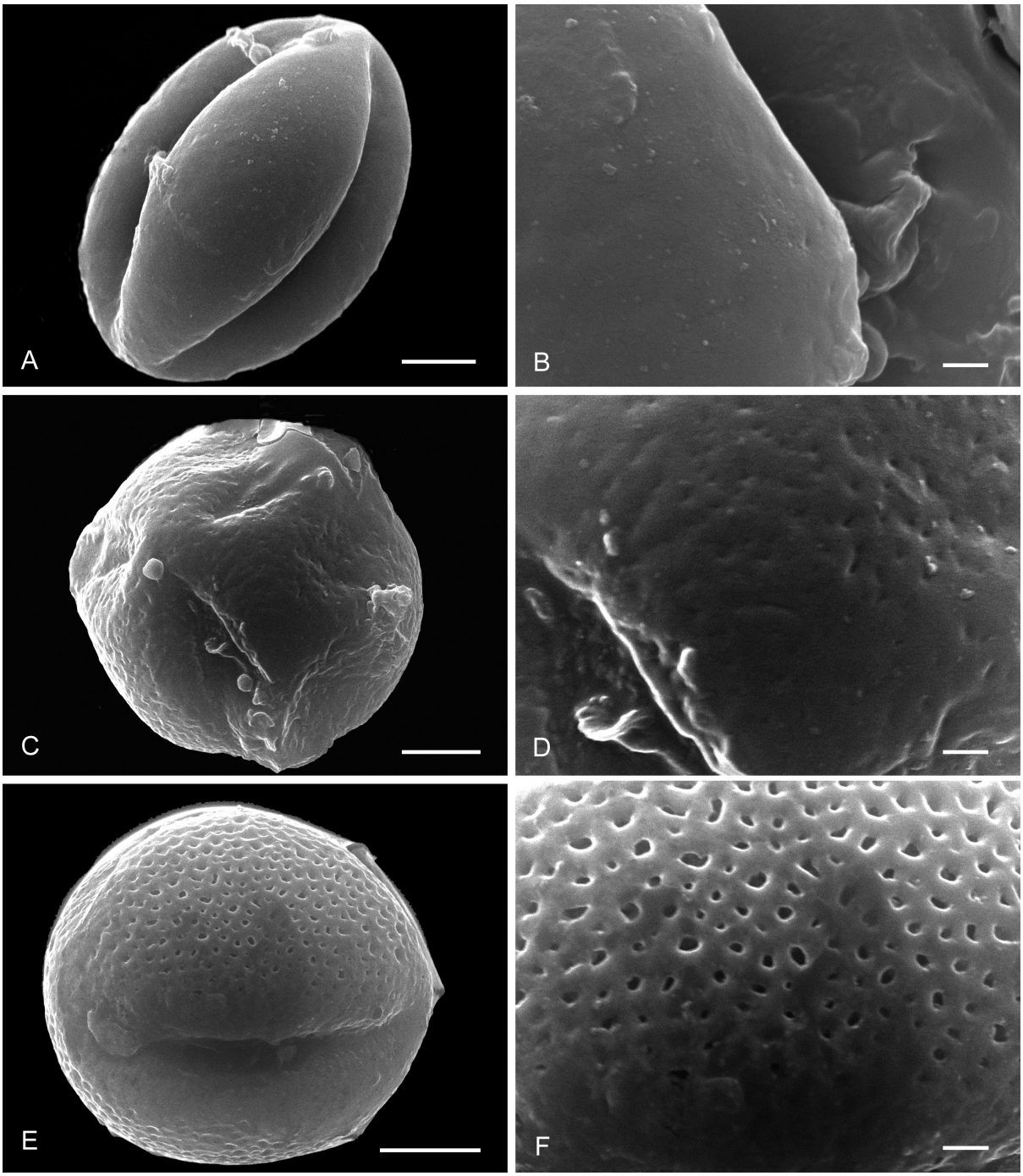

Fig. 1. Pollen grains of *Freylinia* (SEM) – A–D: *F. lanceolata*; E, F – *F. tropica*; A, E: equatorial view; C: polar view; B: sculpture psilate; D: sculpture microperforate; F: sculpture microreticulate. – Scale bars: A, C, E = 5 μm; B, D, F = 1 μm.

Freylinia tropica S. Moore (Fig. 1E–F; 3E–H).

LM — Pollen grains 3-colporate, prolate, spheroidal and occasionally oblate-spheroidal. Amb (polar view) 3-lobed. P = 18.6–30.6 μm, E = 18.6–25.3 μm. Colpi long, 1.3–2.7 μm wide, with distinct, ± level margins, slightly tapering to pointed ends; colpus membrane psilate, sometimes with granules over endoapertures. Endoapertures indistinct, elliptic, 4–7.9 μm long, 2.7 μm wide, covered by margins of colpi. Exine 1.3–1.6 μm thick. Tectum nearly as thick as infratectum. Columellae distinct, thick, short, arranged regularly. Exine sculpture microreticulate.

SEM — Sculpture microperforate and microreticulate. Cells of reticulum small, rounded or elongated, with broad walls. Colpus membrane psilate.

Specimen investigated — South Africa: N Province [Limpopo province]: (Grid Ref. 2427CB), Thabazimbi-Warmbaths road, roadside, dry stream bank, purple form, 25 Sep 1988, *A. Fabian 1197* (MO).

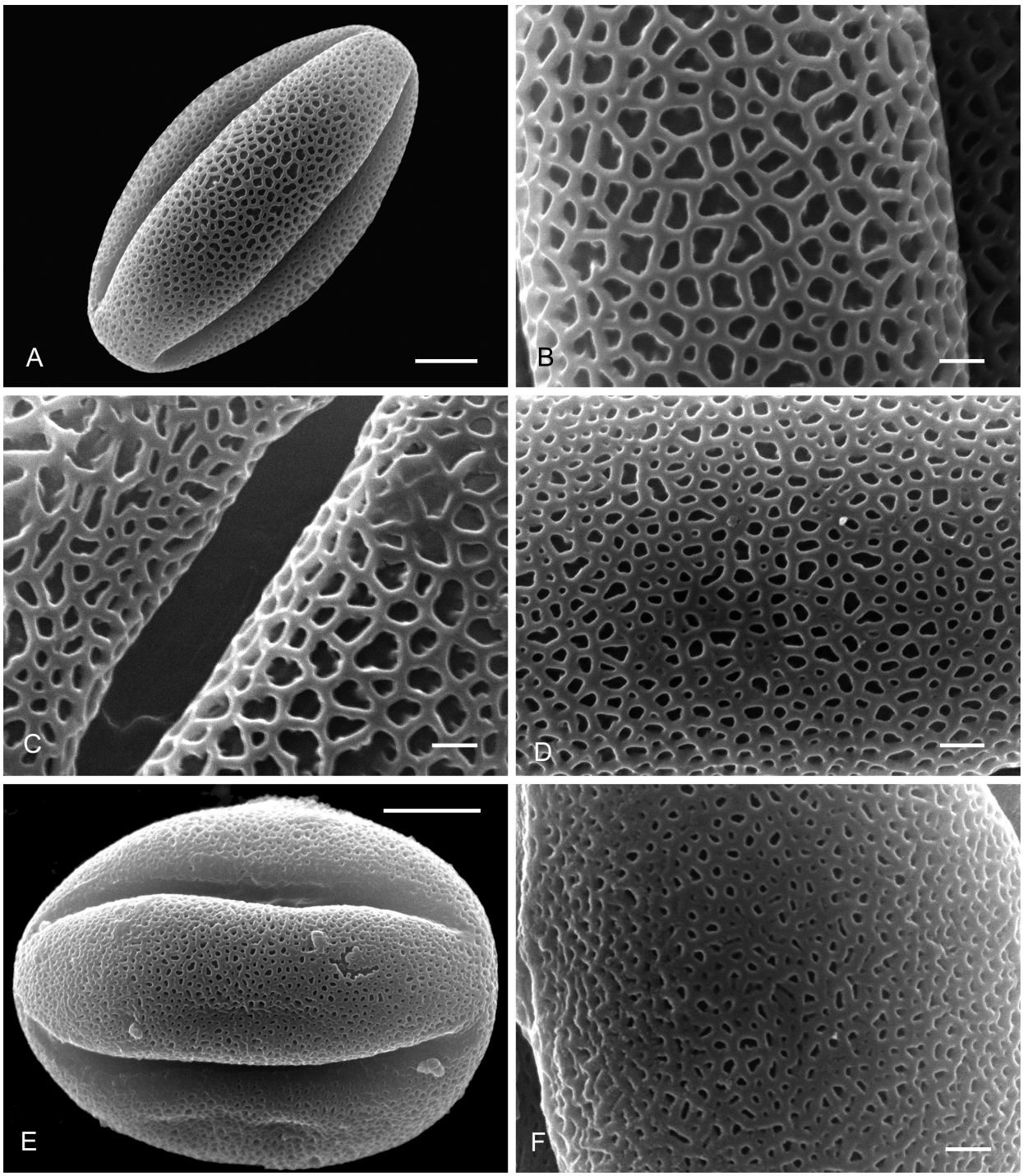

Fig. 2. Pollen grains of *Phygelius* (SEM) – A–C: *P. aequalis*; D–F: *P. capensis*; A, E: equatorial view; B, C: sculpture macroreticulate; D, F: sculpture microreticulate. – Scale bars: A, E = 5 µm; B–D, F = 1 µm.

Phygelius E. Mey. ex Benth.

Phygelius aequalis Harv. ex Hiern (Fig. 2A–C; 3I–L).

LM — Pollen grains 3-colporate, prolate. Amb (polar view) 3-lobed. P=26.6–31.9 µm, E=21.3–25.3 µm. Colpi long, 4 µm wide, with distinct level margins, ends acute; colpus membrane psilate. Endoapertures indistinct, ± circular, 5.3–6.6 µm long, 4–7.9 µm wide. Exine 1.1–2 µm thick. Tectum 2× thinner than infratectum. Columellae distinct, short, arranged regularly. Exine sculpture reticulate.

SEM — Sculpture macroreticulate. Cells of reticulum large, rounded, elongated, rounded-triangular, or rounded-angular. Colpus membrane psilate.

Specimen investigated — South Africa: OVS [Free State province]: (Grid Ref. 2828DA), Kestell, Golden Gate Hoogland Nas. Park, naby klein waterval suid van Ruskamp, 2000 m, Jan 1974, *L. C. C. Liebenberg 8245* (MO).

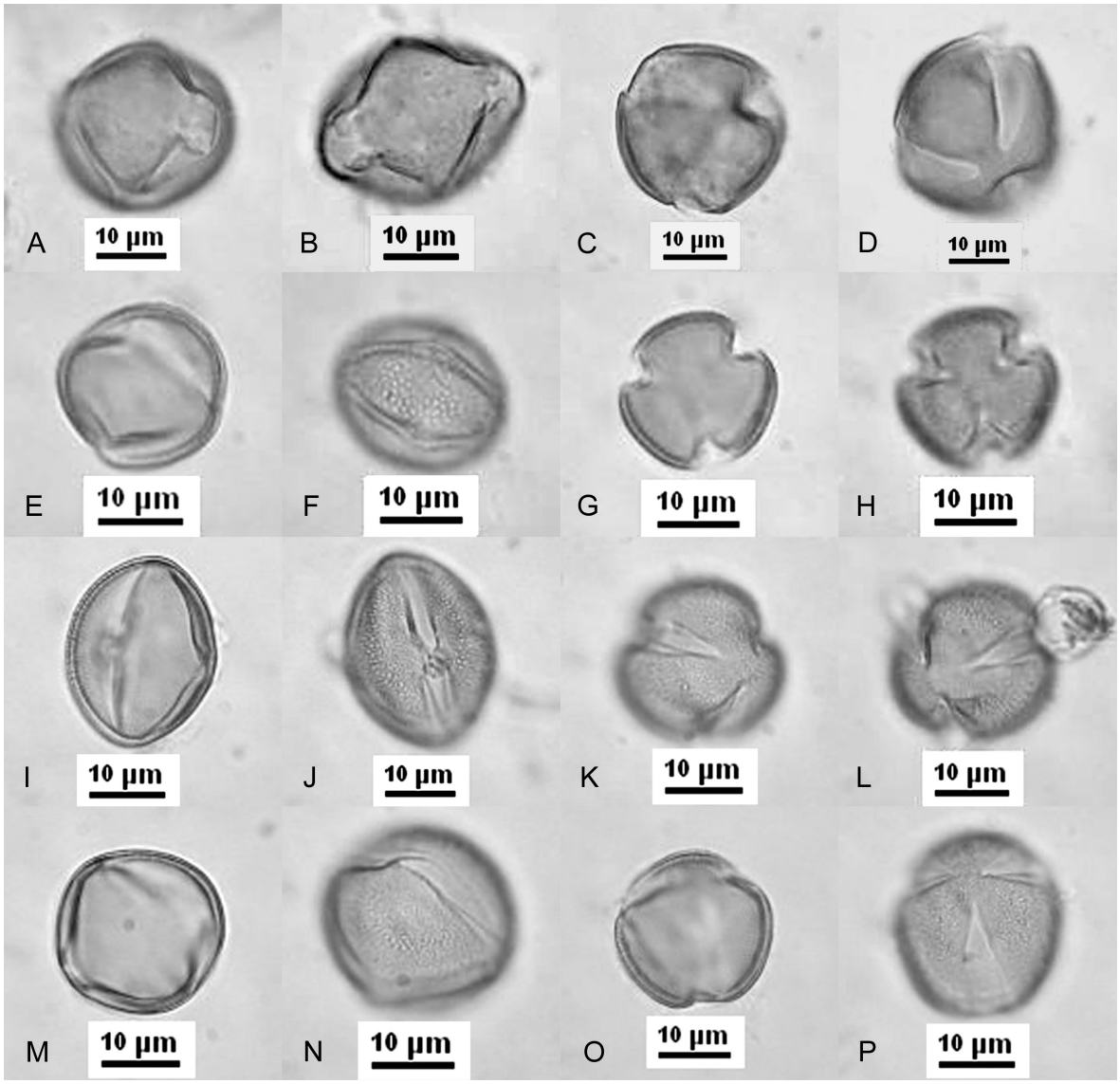

Fig. 3. Pollen grains of *Freylinia* and *Phygelius* (LM) – A–D: *F. lanceolata*; E–H: *F. tropica*; I–L: *P. aequalis*; M–P: *P. capensis*; A, B, E, F, I, J, M, N: equatorial view; C, D, G, H, K, L, O, P: polar view. – Scale bars: A–P = 10 µm.

Phygelius capensis E. Mey. ex Benth. (Fig. 2D–F; 3M–P).

LM — Pollen grains 3-colporate, prolate and occasionally spheroidal or oblate-spheroidal. Amb (polar view) 3-lobed. P=23.9–29.3 µm, E=22.6–26.6 µm. Colpi long, 4–5.3 µm wide, with indistinct margins, ends acute; colpus membrane psilate. Endoapertures distinct or indistinct, elliptic, 6.6–7.9 µm long, 4 µm wide, sometimes covered by margins of colpi. Exine 1.1–1.3 µm thick. Tectum 2× thinner than infratectum. Columellae distinct or indistinct, arranged regularly. Exine sculpture reticulate.

SEM — Sculpture microreticulate. Cells of reticulum small, rounded, elongated, or rounded-angular. Colpus membrane psilate.

Specimen investigated — Lesotho: (2928 CB), Lesobeng area, between the Lesobeng school and Ha Lephoi village on the way to the airstrip, 2125 m, common on slope directly above stream, 3 Mar 1990, *L. Smook 7231* (MO).

Oftia Adans.

Oftia africana (L.) Bocq. (Fig. 4A–B; 6A–D).

LM — Pollen grains 4-colporate, prolate-spheroidal and spheroidal. Amb (polar view) slightly 4-lobed. P=22.6–27.9 µm, E=21.3–27.9 µm. Colpi short, 1.1–1.6 µm wide, with distinct slightly thickened margins, ends rounded; colpus membrane psilate. Endoapertures distinct, elongated, rectangular, 6.6–9.3 µm long, 2.4–4 µm wide. Exine 1.1–1.3 µm thick. Columellae indistinct or sometimes visible. Exine sculpture psilate with thin pleats sparsely arranged, rarely microreticulate.

SEM — Sculpture psilate and foveolate. Colpus membrane psilate.

Specimen investigated — South Africa: Western Cape province: Cape Peninsula, Wynberg Hill, Jun 1950, *N. S. Pillans 10046* (MO).

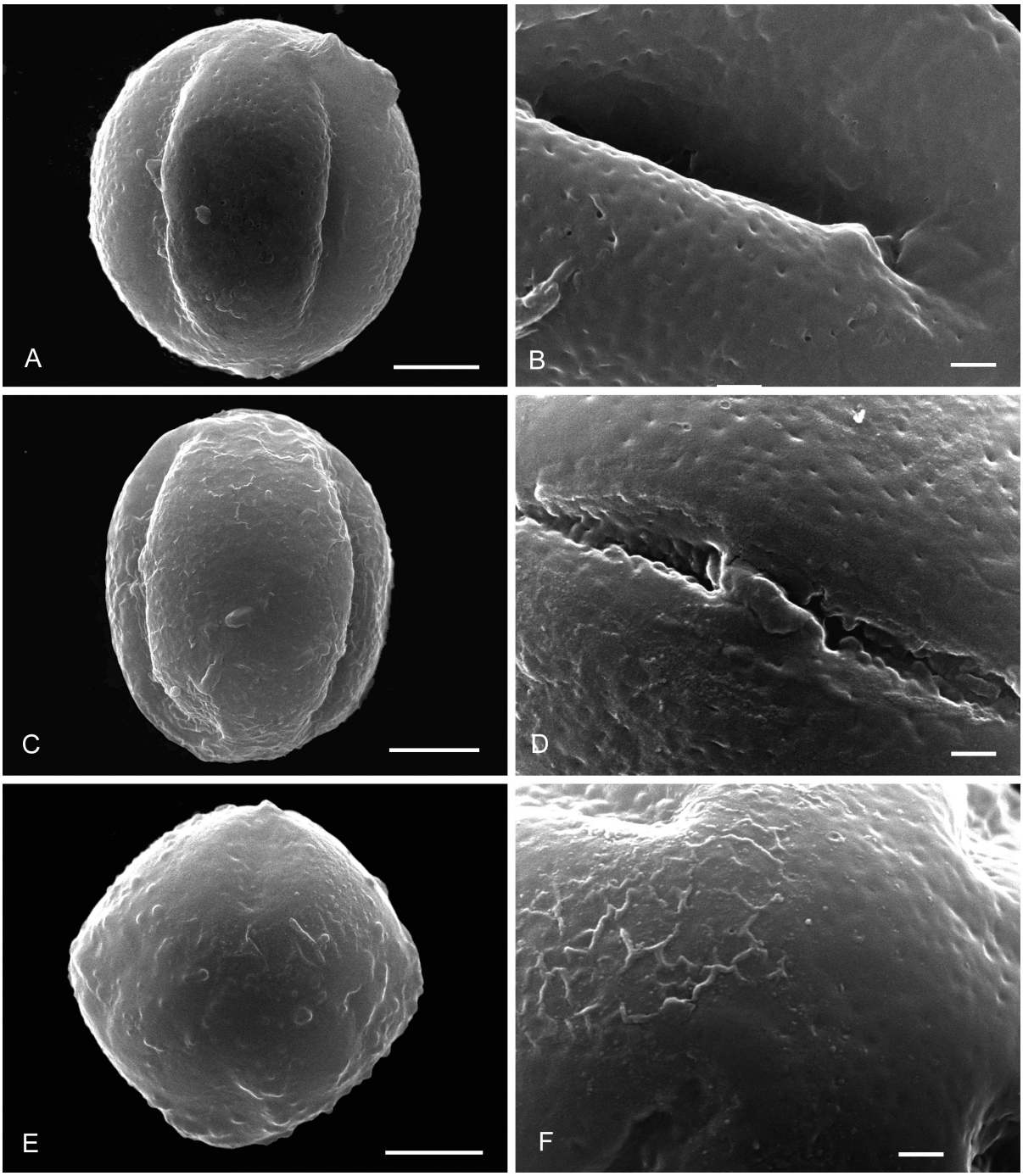

Fig. 4. Pollen grains of *Oftia* (SEM) – A, B: *O. africana*; C–F: *O. revoluta*; A, C: equatorial view; E: polar view; B, D: sculpture psilate and foveolate; F: sculpture psilate and rough. – Scale bars: A, C, E = 5 µm; B, D, F = 1 µm.

Oftia revoluta (E. Mey.) Bocq. (Fig. 4C–F; 6E–H).

LM — Pollen grains 4-colporate, oblate-spheroidal. Amb (polar view) slightly 4-lobed. P=21.3–25.3 µm, E=21.3–27.9 µm. Colpi short, 1.6–2.4 µm wide, with indistinct level margin, ends rounded; colpus membrane psilate. Endoapertures distinct, elongated, rectangular, 6.6–9.3 µm long, 2.7 µm wide. Exine 1.1–1.6 (2) µm thick. Exine layers indistinct, columellae invisible. Exine sculpture psilate, with thin sparsely arranged pleats.

SEM — Sculpture psilate and rough, sometimes foveolate. Colpus membrane psilate, sometimes granulate.

Specimen investigated — South Africa: Northern Cape province: Namaqualand, pipeline track, 12 km from Nababiep towards Spektakelberg, clay substrate with many rocks, 15 Oct 1974, *P. Goldblatt 3064* (MO).

Teedia Rudolphi

Teedia lucida (Sol.) Rudolphi (Fig. 5A–F; 6I–L).

LM — Pollen grains 4-colporate, oblate-spheroidal. Amb (polar view) 4-lobed. P=19.9–25.3 µm, E=22.6–27.9 µm. Colpi short, 2–4 µm wide, with distinct margins, ends rounded; sometimes two colpi fused in one

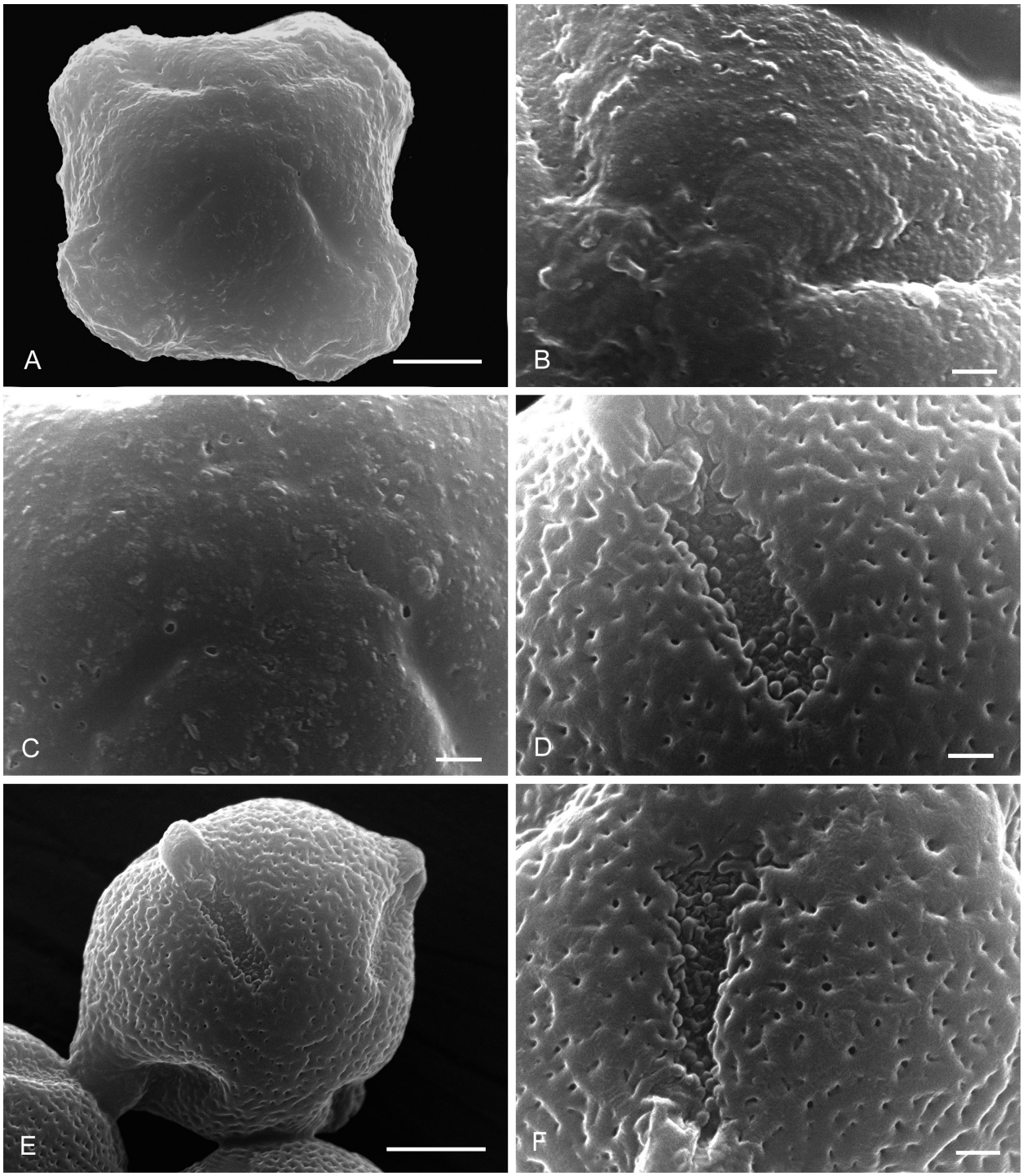

Fig. 5. Pollen grains of *Teedia* (*T. lucida*) (SEM) – A: polar view; E: equatorial view; B, C: sculpture rough with microperforations; D, F: sculpture foveolate. – Scale bars: A, E = 5 μm; B–D, F = 1 μm.

on apocolpia; colpus membrane psilate and granulate. Endoapertures distinct, longitudinally elongated, square or rectangular, 3.3–5.3 μm long, 5.3–6.6 μm wide. Exine 1.1–1.6 μm thick. Exine layers indistinct, columellae occasionally distinct, short, arranged regularly. Exine sculpture perforate.

SEM — Sculpture psilate, rough, occasionally with small perforations or foveolate. Colpus membrane psilate, granulate.

Specimens investigated — South Africa: Eastern Cape province: Mountain Drive, overlooking Monument building, above by-pass, 3326 BC, 33°19'23"S, 26°31'58"E, 600 m, disturbed ground, 4 Nov 2001, *P. B. Phillipson 5332 with P. Kornall* [*Kornhall*?] (MO). — Northern Cape province: 3020 (Loeriesfontein) CD, Kubiskou mountain, W of Loeriesfontein, 30°50'04"S, 19°21'16"E, 4502 feet, in dolerite outcrop, 14 Sep 2006, *P. Goldblatt & L. J. Porter 12828* (MO). — Western

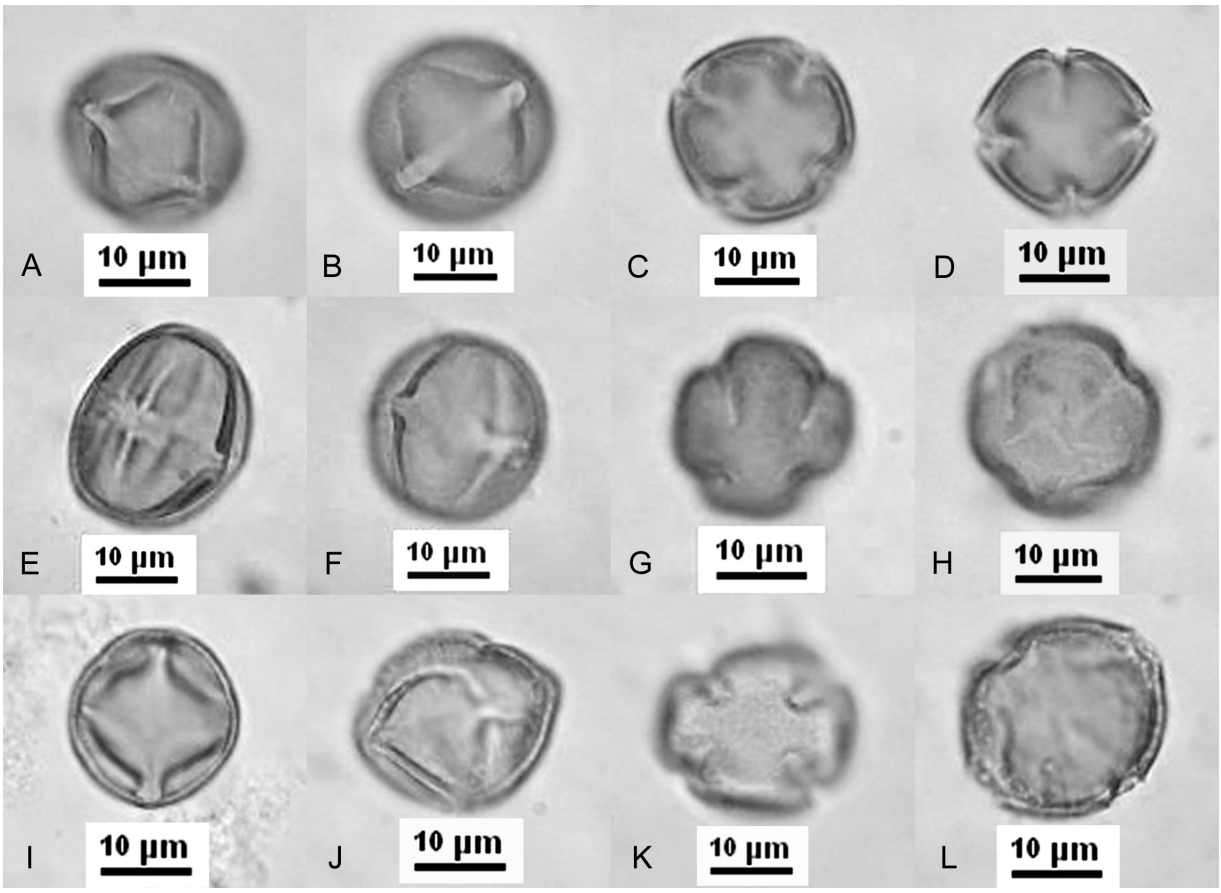

Fig. 6. Pollen grains of *Oftia* and *Teedia* (LM) – A–D: *O. africana*; E–H: *O. revoluta*; I–L: *T. lucida*; A, B, E, F, I, J: equatorial view; C, D, G, H, K, L: polar view. – Scale bars: A–L = 10 µm.

Cape province: 3320 (Montagu) CA, top of Ouberg Pass, sandstone rocks, in rock crevices, 27 Sep 1997, *P. Goldblatt* & *J. Manning 10772* (MO).

Discussion

The data obtained demonstrated that pollen grains of the studied taxa are different and can be distinguished at the levels of genera and species.

According to their aperture types, pollen grains in species of *Freylinia* and *Phygelius* are similar. Here the pollen grains have long colpi and a psilate colpus membrane, but differ in other characters. In particular, pollen grains of the two studied species of *Phygelius* have wide colpi with acute ends, but their endoapertures differ in shape: circular in *P. aequalis* and elliptic in *P. capensis*. Also, pollen grains of these species differ in their exine sculpture: macroreticulate in *P. aequalis* and microperforate and microreticulate in *P. capensis*.

The two species of the genus *Freylinia* differ in their colpi structure, endoaperture shape, and exine sculpture. On the one hand, the structure of apertures and sculpture of pollen grains of *F. tropica* are similar to those in *Phygelius capensis*. But on the other hand, they differ visibly in the width of their colpi.

Pollen grains of *Oftia* and *Teedia* (phylogenetically sister crown groups, according to Oxelman & al. 2005) are similar in their aperture types, all having short colpi with rounded ends, and psilate, rough, and foveolate exine sculpture. However, there are some differences between these genera: the grains in *Teedia* have wider colpi and somewhat smaller (shorter but wider) endoapertures than those in *Oftia*. Moreover, in *Teedia* two colpi are sometimes fused on apocolpia, a feature never observed in *Oftia*. The two species of *Oftia* vary in the width of their colpi.

The patterns of all observed pollen characters seem to be unique for each of the studied species. It means that pollen characters, when looked at in detail, can be used to separate certain species in the tribe.

According to molecular phylogenetic data (Oxelman & al. 2005), *Oftia* and *Teedia* are included in the same clade as sister subclades. Palynomorphological data support the hypothesis of close relationships between these two genera, as shown above. The genus *Freylinia* is a sister group to the *Oftia+Teedia* clade, more distantly related to either of these genera than they are to each other, as also supported by our data on morphology of pollen grains. The studied members of the crown clade (*Oftia+Teedia*) have four colpi (probably an advanced character in the tribe), whereas *Freylinia* and *Phygelius* have tricolpate

pollen grains. The *Phygelius* branch is sister to the clade containing *Freylinia* and the *Oftia+Teedia* clade.

In conclusion, where genera are concerned, although some characters are shared, if all details of palynomorphology are taken into account, they can be used to separate the genera.

The new palynomorphological data are rather consistent with the results of molecular phylogenetic studies. Apparently being a rather early-branching group of *Scrophulariaceae*, the *Teedieae* provide insights into the further morphological evolution of pollen grains in the whole family. We believe that in this tribe some ancestral pollen types and characters are preserved from the times of early evolutionary radiation of the family. For instance, representatives of *Teedieae* usually have the colporate aperture type, which probably should be considered as ancestral in *Scrophulariaceae.* Species of this tribe demonstrate rather primitive characters of their pollen grains: smooth, rough, perforate, or microreticulate exine sculpture and smooth, rarely granulate, sculpture of colpi membranes. However, some taxa of the tribe (e.g. *Phygelius*) already demonstrate some advanced pollen traits more peculiar to crown *Scrophulariaceae*. Pollen grains of *P. aequalis* have well-developed reticulate sculpture, which is more characteristic of pollen grains of apparently more evolutionarily advanced tribes of the family, such as *Limoselleae* and *Scrophularieae*.

Looking beyond the *Teedieae*, it is interesting to note that pollen grains in the tribe *Buddlejeae* are also characterized mainly by the colporate pollen type with smooth, rough, perforate, or reticulate surface sculpture and smooth sculpture of colpi membranes (Tsymbalyuk & Mosyakin 2013). In these characters, these two tribes are similar. Some representatives of *Buddlejeae* (e.g. *Gomphostigma virgatum* (L. f.) Baill.) also have a well-developed reticulate sculpture (Tsymbalyuk & Mosyakin 2013). Such pollen morphology patterns and character distribution in *Buddlejeae* are very similar to those found in *Teedieae*, which probably indicates close phylogenetic links between these clades, or even their parallel evolutionary trends. Moreover, the palynomorphological characters and patterns of their distribution in *Teedieae* and *Buddlejeae* can probably be viewed as ancestral (or, at least, close to ancestral) for those in more advanced clades of *Scrophulariaceae.*

Thus, the study reported here demonstrated rather good correlation of the main morphological characters of pollen grains in *Teedieae* and related tribes with new molecular phylogenetic data. In order to reveal the pathways of evolution of pollen grains in *Scrophulariaceae* in more detail, it would be also important to compare the data reported here with similar data on representatives of other early-branching lineages of the family, especially tribes *Aptosimeae*, *Leucophylleae*, *Myoporeae* and *Hemimerideae*. We already have palynomorphological data on key taxa of these groups. Information on pollen morphology in these tribes, a comparative analysis, and discussion on possible ancestral character states of pollen grains in *Scrophulariaceae* will be provided in a separate article (in preparation).

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