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ORIGINAL ARTICLE

Pollen morphology of selected species of the genera *Chrysodracon* and *Dracaena* (Asparagaceae, subfamily Nolinoideae) and its systematic implications

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Abstract
Pollen grains of 3 species from the genus *Chrysodracon* and 20 species from the genus *Dracaena* were examined by light, scanning electron and fluorescence microscopy. The basic shape of the pollen grains is subprolate and prolate, but prolate-spheroidal pollen grains may also be found. Pollen of *Chrysodracon* and *Dracaeana* is dispersed as monads, rarely as dyads. In terms of size, the pollen grains studied were classified as medium-sized and large. There are two different types of apertures: monosulcate and monoulcerate in *Dracaena* and monoulcerate in *Chrysodracon*. The surface of the non-apertural areas is psilate-perforate, irregularly folded, microreticulate and fossulate. Ornamentation of the apertural region is microreticulate, microreticulate-baculate, baculate, psilate-perforate, psilate-perforate-verrucate, granulate and irregularly folded. Irregular perforations are present, and the wall structure is tectate-columellate. Our results suggest that some species of *Chrysodracon* and *Dracaena* may be separated based on their pollen grain micromorphology on the distal region.

Keywords *Chrysodracon* · *Dracaena* · Micromorphology · Monocot · Palynology · Taxonomy

Introduction

The systematics of the dracenoid clade of Asparagaceae (APG III 2009) is so far not completely resolved. The genus *Dracaena* Vand. and its two other closely allied genera *Pleomele* Salisb. and *Sansevieria* Thunb. are recognized differently by various authors.

Observed similarity in floral morphology induced some authors to include the genus *Sansevieria* into *Dracaena* (e.g., Bos 1984, 1998). Recent molecular phylogenetic studies show that *Sansevieria* is nested within *Dracaena* sensu lato (Lu and Morden 2014). However, other researchers have treated *Sansevieria* as a separate taxon at genetic rank (Brown 1914; Jankalski 2003; Wiland–Szymańska and Klimko 2005; Mansfeld 2015) due to differences from *Dracaena* in morphological, palynological and carpological characters.

The genus *Dracaena* was founded in 1768 by Vandelli upon *Dracaena draco* L. (Brown 1914). Due to dissimilarities in the structure of flowers, the species described in this genus were allocated by Brown into two genera: *Dracaena* sensu stricto with divided tepals and filaments of stamens centrally thickened and *Pleomele* Salisb., characterized by a long perianth tube and filiform stamina filaments (Brown 1914). This division was not generally agreed upon, and species with the *Pleomele* characters were generally referred to as *Dracaena* (e.g., Bos 1998). The two genera were combined by Jankalski (2008), who recognized *Dracaena* as a genus with two subgenera: subg. *Dracaena* and subg. *Pleomele*. The available molecular data support unification of these taxa into one genus *Dracaena* (Lu and Morden 2014). These genetic concepts are those currently accepted within the dracenoids, with *Dracaena* containing both species of the dragon tree group with free tepals and the mesophytic group with long-tubed flowers.

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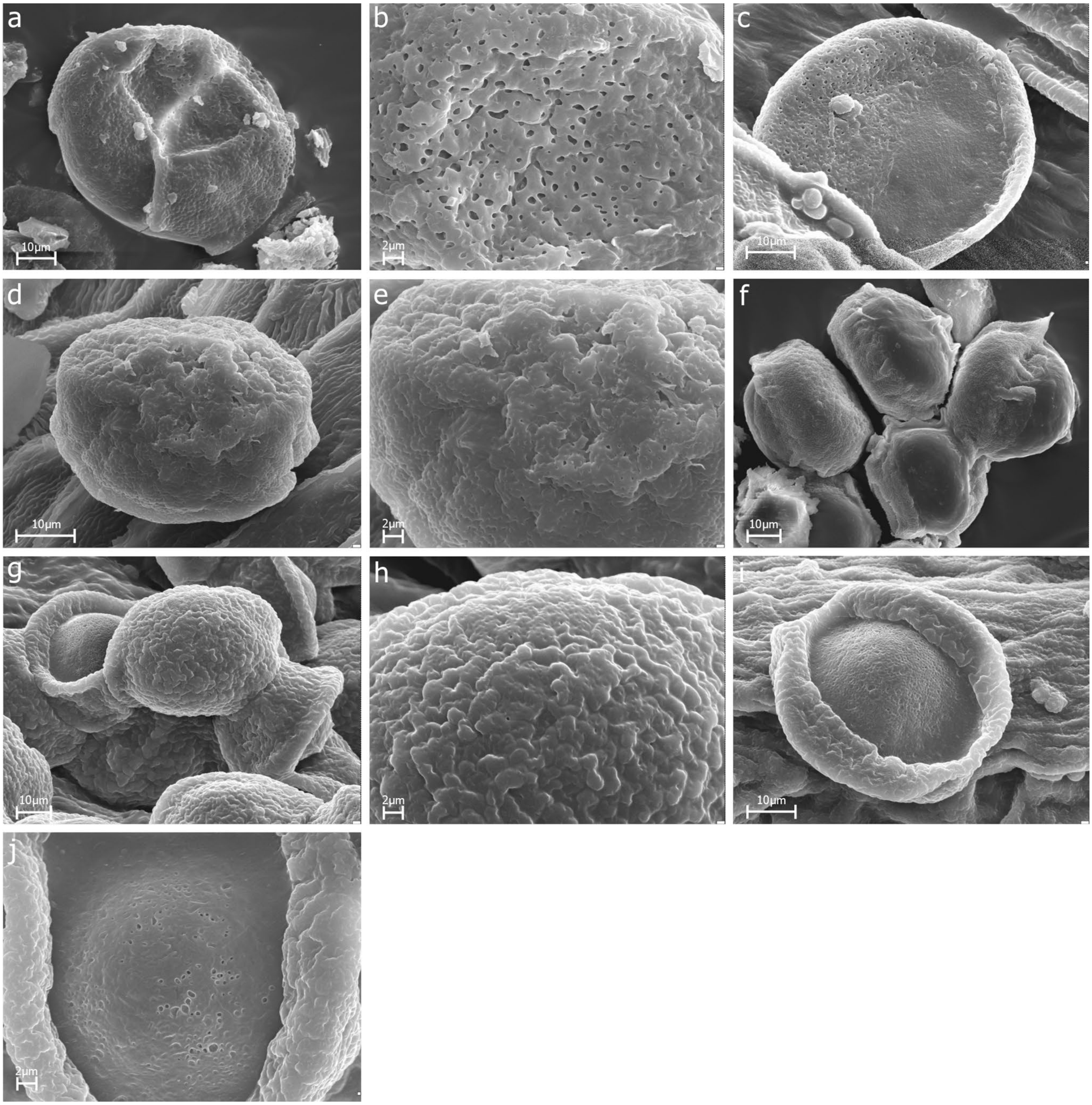


Fig. 1 SEM micrographs of pollen grains of *Chrysodracon* species studied. **a-c** *Chrysodracon aurea*. **a** In proximal view. **b** Exine surface, enlargement of **a. c** In distal view. **d-f** *Chrysodracon fernaldii.* **d** In proximal view. **e** Exine surface, enlargement of **d**. **f** In lateral and distal view. **g- j** *Chrysodracon forbesii.* **g** In proximal and distal view. **h** Exine surface, enlargement of **g**. **i** In distal view. **j** Exine surface, enlargement of **i**

The third group recognized by Jankalski (2008) was *Dracaena* subg. *Chrysodracon* Jankal. composed of the species included before into *Pleomele* and endemic to the Hawaii Islands. As they are characterized by unique floral characters and form a distinct sister clade to other species of dracenoids, they were delineated as a separate genus *Chrysodracon* P.L.Lu & Morden by Lu and Morden (2014). Concluding, in this paper, we recognize three genera within the dracenoid clade: *Dracaena, Sansevieria* and *Chrysodracon.*

Pollen characters, e.g., aperture type, variation in exine ornamentation and wall structure, have frequently been

Table 1 Quantitative features of pollen grains in *Chrysodracon* and *Dracaena* species with the results of one-way ANOVAs

Features species	Length of long axis (LA)			Length of short axis (SA)			LA/SA ratio		
	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD
Chrysodracon aurea	45.8	74.1	60.2 ± 7.2	21.2	56.5	40.8 ± 8.3	1.1	2.6	1.53 ± 0.35
C. fernaldii	45.8	63.5	51.8 ± 4.0	24.7	56.5	44.2 ± 6.5	1.0	1.8	1.19 ± 0.17
C. forbesii	49.4	70.6	60.0 ± 4.0	24.7	60.0	45.9 ± 7.3	1.0	2.0	1.34 ± 0.20
Dracaena afromontana	38.8	54.3	47.6 ± 4.9	28.6	45.7	40.0 ± 5.1	0.7	1.7	1.21 ± 0.21
D. aletriformis	56.5	74.1	64.4 ± 4.6	38.8	67.1	57.0 ± 6.2	1.0	1.6	1.14 ± 0.15
D. americana	24.7	35.3	30.4 ± 3.0	17.6	31.7	22.9 ± 4.3	1.0	1.8	1.36 ± 0.23
D. arborea	52.9	70.6	62.7 ± 5.5	35.3	63.5	48.6 ± 7.7	1.0	1.7	1.32 ± 0.21
D. aubryana	56.5	70.6	64.3 ± 3.0	42.4	63.5	53.8 ± 7.3	1.0	1.6	1.22 ± 0.20
D. cambodiana	28.2	42.4	36.4 ± 3.0	21.2	35.3	27.3 ± 4.1	1.0	2.0	1.40 ± 0.26
D. camerooniana	52.9	77.6	65.5 ± 6.4	38.8	70.6	55.9 ± 6.8	1.0	1.6	1.18 ± 0.15
D. conferta	42.4	67.1	56.6 ± 6.3	28.2	56.5	40.5 ± 7.2	1.1	2.0	1.42 ± 0.22
D. deremensis	49.4	67.0	57.5 ± 4.6	28.2	56.5	46.7 ± 6.8	1.0	1.7	1.25 ± 0.19
D. draco	35.3	45.8	39.8 ± 3.3	21.2	35.3	28.2 ± 3.4	1.1	1.8	1.43 ± 0.23
D. ellenbeckiana	38.8	49.4	45.0 ± 2.9	24.7	42.4	34.5 ± 4.6	1.0	1.7	1.33 ± 0.17
D. fragrans	28.2	60.0	50.1 ± 7.0	21.2	49.4	38.1 ± 7.4	1.0	2.5	1.36 ± 0.31
D. mannii	56.5	81.2	66.9 ± 5.9	35.3	67.1	51.1 ± 8.8	1.0	1.9	1.35 ± 0.25
D. multiflora	38.8	77.6	61.7 ± 8.7	28.2	67.1	47.7 ± 10.7	1.0	2.3	1.37 ± 0.33
D. ombet	24.7	31.7	28.4 ± 1.9	14.1	28.2	22.6 ± 2.8	1.0	2.5	1.28 ± 0.25
D. pendula	56.4	81.2	74.6 ± 5.2	38.8	81.2	62.0 ± 11.2	1.0	1.9	1.24 ± 0.25
D. reflexa	38.8	60.0	51.5 ± 4.8	28.2	52.9	43.5 ± 6.1	1.1	1.5	1.20 ± 0.12
D. schizantha	24.7	31.7	28.0 ± 2.5	14.1	24.7	21.0 ± 2.9	1.0	2.0	1.35 ± 0.22
D. serrulata	28.2	42.4	34.9 ± 3.5	17.6	31.7	27.3 ± 3.8	1.0	1.6	1.30 ± 0.17
D. surculosa var.*surculosa*	38.8	56.5	49.8 ± 4.1	31.7	52.9	40.2 ± 5.6	1.0	1.5	1.26 ± 0.17
ANOVA	F = 975317.0 $P < 0.05$			F = 271524.4 $P < 0.05$			F = 1361.4 $P < 0.05$		

regarded as systematically significant in monocotyledons above and below the family level (Zavada 1983; Linder and Ferguson 1985; Furness and Rudall 2001). Palynology has been little studied for *Dracaena*, but it is of considerable importance in systematic studies generally. There are only few works concerning pollen morphology of *Dracaena* (Erdtman 1952, 1960; Meier and Yaroshevskaya 1973; Ojeda et al. 1984; Guang-Zheng 1993; Ojeda and Ludlow-Wiechers 1995; Bos 1998; Rudall et al. 2000; Mwachala 2005; Patil and Pai 2011). There is also one publication describing pollen of two extinct *Dracaena* species from the Neogene (Van Campo and Sivak 1976). The pollen of the closely related *Sansevieria* was also studied by several authors (Ojeda et al. 1984; Ojeda and Ludlow-Wiechers 1995; Buchner and Halbritter 2010; Klimko et al. 2017). To date, no reports have been published concerning pollen of the genus *Chrysodracon*.

The hypothesis in the present study is that pollen grains of the dracenoid clade species exhibit a greater variation than it has been reported in literature. The main goal of this study was: 1) to describe variation in pollen grain morphology of the 3 species of *Chrysodracon* and 20 species of *Dracaena* and 2) to illustrate the microstructure of the pollen grains with the aim of providing new diagnostic features for their characterization and to determine their characters of systematic importance.

Materials and methods

Pollen was obtained from herbarium specimens deposited at the Royal Botanic Gardens, Kew (K). The samples represent 20 species of *Dracaena*, including 8 species from the dragon tree group. Moreover, 3 species of *Chrysodracon* were examined. The scanning electron microscope (SEM) observations were made on pollen grains which were dried, while for light microscope (LM), the pollen grains were macerated with 10% KOH (Dyakowska 1959; Frederiksen 1978). A sample consisted of 30 mature pollen grains. In total, 750 pollen grains were examined. The pollen terminology was adopted from Faegri and Iversen (1989) and Hesse et al. (2007). The shape classification followed that

Table 2 Qualitative features of pollen grains in *Chrysodracon* and *Dracaena* species

Features species	Size class	Basic shape based on mean LA/SA ratio	Aperture shape	Exine ornamentation of non-apertural areas (proximal surface)	Exine ornamentation of apertural areas (distal surface)
Chrysodracon aurea	medium, large	prolate	ulcerate	psilate-perforate	granulate
C. fernaldii	medium, large	subprolate	ulcerate	psilate-perforate, irregularly folded	psilate-perforate
C. forbesii	medium, large	prolate	ulcerate	fossulate	microreticulate, psilate-perforate
Dracaena afromontana	medium, large	subprolate	sulcate/ulcerate	fossulate	psilate-perforate
D. aletriformis	large	subprolate	sulcate	psilate-perforate, irregularly folded	microreticulate
D. americana	medium, large	prolate	sulcate	fossulate	irregularly folded
D. arborea	large	subprolate	sulcate/ulcerate	psilate-perforate	psilate-perforate
D. aubryana	large	subprolate	sulcate/ulcerate	psilate-perforate	microreticulate-baculate
D. cambodiana	medium, large	prolate	sulcate/ulcerate	psilate-perforate, folded	psilate-perforate
D. camerooniana	large	subprolate	sulcate	psilate-perforate	psilate-perforate-verrucate
D. conferta	medium, large	prolate	sulcate	psilate-perforate	psilate-perforate-verrucate
D. deremensis	medium, large	subprolate	sulcate	microreticulate	psilate-perforate
D. draco	medium, large	prolate	sulcate	microreticulate	psilate-perforate
D. ellenbeckiana	medium, large	subprolate	sulcate	psilate-perforate, folded	psilate-perforate
D. fragrans	medium, large	prolate	sulcate	fossulate	microreticulate, baculate
D. mannii	large	prolate	sulcate/ulcerate	psilate-perforate, fossulate	psilate-perforate
D. multiflora	medium, large	subprolate	sulcate	fossulate	irregularly folded
D. ombet	medium, large	subprolate	sulcate	microreticulate	psilate-perforate
D. pendula	large	subprolate	sulcate	psilate-perforate	microreticulate
D. reflexa	medium, large	subprolate	sulcate	psilate-perforate, fossulate	microreticulate
D. schizantha	medium, large	prolate	sulcate	microreticulate	psilate-perforate
D. serrulata	medium, large	subprolate	sulcate	microreticulate	psilate-perforate-verrucate
D. surculosa var.*surculosa*	medium, large	subprolate	sulcate/ulcerate	psilate-perforate, folded	psilate-perforate-verrucate

of Erdtman (1952). The size classification followed that of Dyakowska (1959). Pollen grains were analyzed for three quantitative traits, i.e., length of the long axis (LA), length of the short axis (SA) and the LA/SA ratio as well as the following qualitative traits: pollen outline and shape and exine ornamentation on the proximal and distal sides.

Light, scanning electron and fluorescence microscopy

The observations were carried out under an Olympus BX 43 light microscope equipped with a camera lucida. The SEM micrographs were taken using a Zeiss EVO 40 microscope (Carl Zeiss, Jena, Germany) at an accelerating voltage of 10-15 kV, at the Electron and Confocal Microscopy Laboratory, Faculty of Biology, Adam Mickiewicz University in Poznań. Prior to the observations, the prepared material was sputtered with gold using an SCB 050 ion sputter. The study was documented with photographs taken during observations, primarily at magnifications ranging from × 2.500 to x 3.500 for shape and x 10.000–20.000 for exine sculpture of the pollen grains. The observations were carried out in an Olympus BX 43 light microscope equipped with a camera lucida. The pollen from dehiscent anthers was fixed in a mixture of glycerol and ethanol (1:1; v/v) and then dehydrated stepwise with a graded ethanol series and finally embedded in Epon (Meek 1976). Next, embedded samples were cut with a Tesla 490A microtome into thin (3 µm) sections and glued to the slides with Haupt adhesive (1% gelatin in water with 2% phenol crystals and 15% glycerin). Unstained sections were examined under a Zeiss Lab. A1 fluorescence microscope (FM) in UV light (wavelength 365 nm) for exine structure analyses.

Statistical analysis

The minimal and maximal values as well as arithmetical means and standard deviations were calculated for

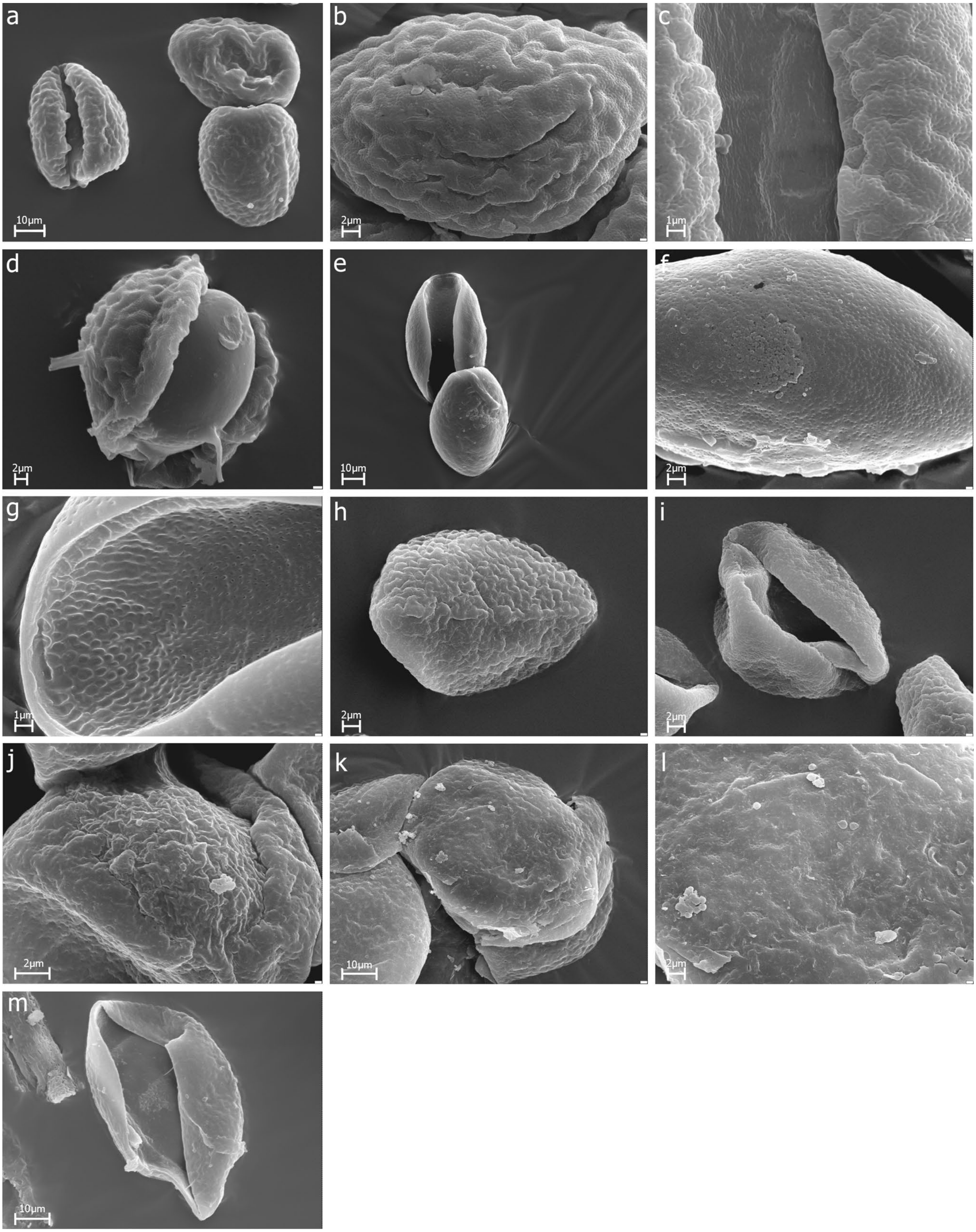


Fig. 2 SEM micrographs of pollen grains of *Dracaena* species studied. **a-d** *Dracaena afromontana.* **a** In proximal and distal view. **b** Exine surface of proximal surface. **c** Distal surface. **d** Laterally germinating pollen. **e–g** *Dracaena aletriformis.* **e** In proximal and distal view. **f** Exine surface, enlargement of **e**. **g** Exine surface, enlargement of **e**. **h-j** *Dracaena americana.* **h** In proximal view. **i** In distal view. **j** Distal surface. **k-m** *Dracaena arborea.* **k** In proximal view. **l** Exine surface, enlargement of **k**. **m** In distal view

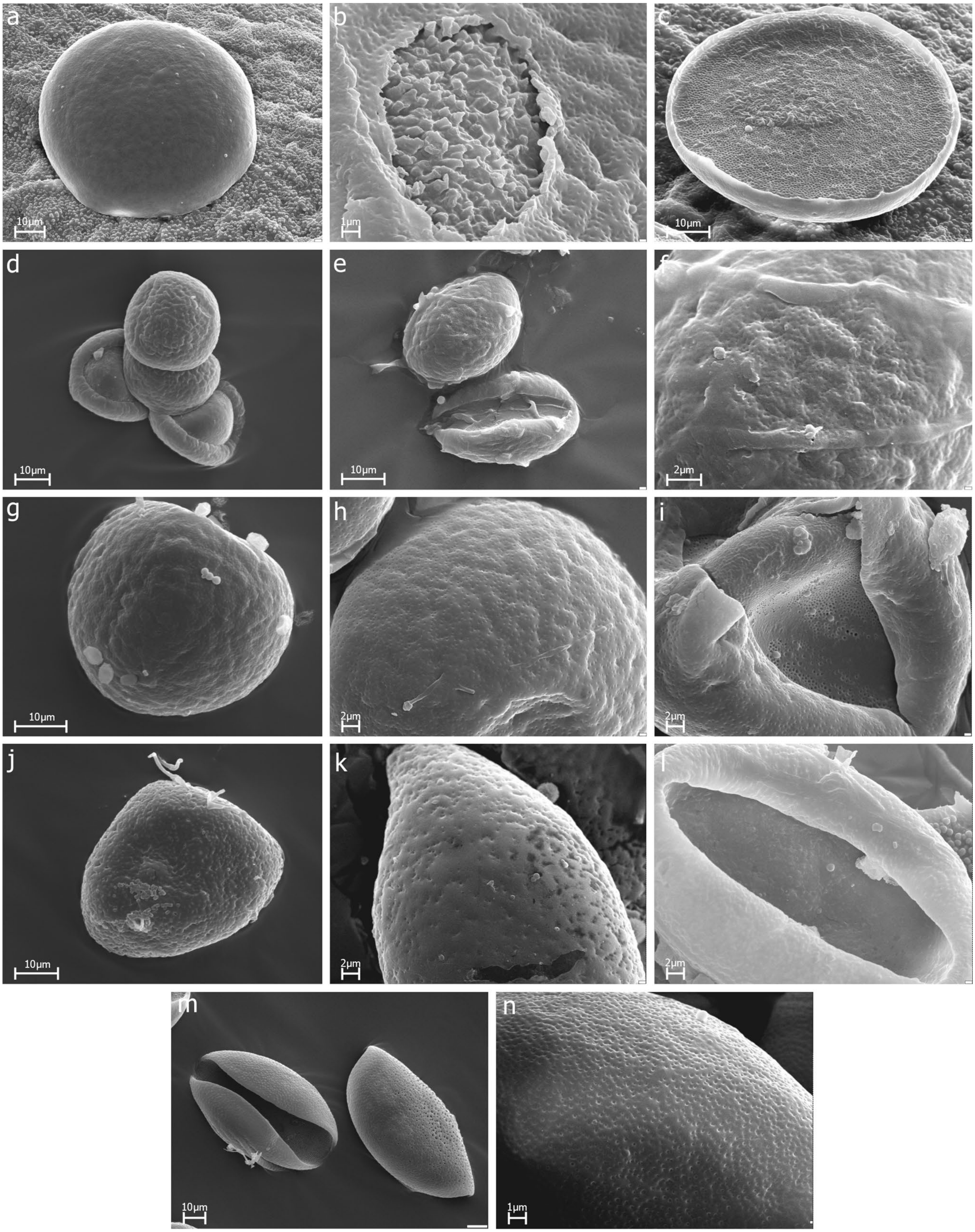


Fig. 3 SEM micrographs of pollen grains of *Dracaena* species studied. **a-c** *Dracaena aubrayna.* **a** In proximal view. **b, c** Distal surface. **d-f** *Dracaena cambodiana.* **d, e** In proximal and distal view. **f** Exine surface, enlargement of **e**. **g-i** *Dracaena camerooniana.* **g** In proximal view. **h** Exine surface, enlargement of **g**. **i** In distal view. **j-l** *Dracaena conferta.* **j** In proximal view. **k** Proximal surface. **l** In distal view. **m, n** *Dracaena deremensis.* **m** In proximal and distal view. **n** Exine surface, enlargement of **m**

quantitative characteristics. Prior to the statistical analyses, the normality and homogeneity of variance for each morphological feature was checked using Shapiro–Wilk's test and Levene's test. Because some of the data did not meet the necessary assumptions, all the data were logarithmically transformed. The one-way ANOVAs and Tukey's HSD tests was used to examine differences in the mean values among the characters of studied species. In ANOVA, the homoscedasticity was checked based on scatter plots between the predictors and the residuals. Statistical analyses were performed using Statistica 12.5 for Windows software.

Specimens investigated included: *Chrysodracon aurea* (H.Mann) P.L.Lu & Morden–Hawaiian Islands, Kauai, *Heller 2362* (K); *C. fernaldii* (H.St.John) P.L.Lu & Morden–Hawaiian Islands, Kamodu, *Cowan 22595* (K); *C. forbesii* (O.Deg.) P.L.Lu & Morden–Hawaiian Islands, *St. John 20230* (K); *Dracaena afromontana* Mildbr.–Tanzania, SW Kilimanjaro, *Haarer 1169* (K); *D. aletriformis* (Haw.) Bos–South Africa, Hort. Kew, 11/1866 (K); *D. americana* Donn.Sm.-Belize, El Cayo District, *Gentle 2005* (K); *D. arborea* K.Koch–Equatorial Guinea, Bioco, Malaba, *Carvalho 2083* (K); *D. aubryana* Brongn. ex É.Morren–Cameroon, 17 km NE of Deng Deng, *Breteler 994* (K); *D. cambodiana* Pierre ex Gagnep.–Thailand, Baw Re Kanburi, *Put 205* (K); *D. camerooniana* Baker–Congo Republic, Haut-Katanga, Keyberg (Kisanga) near Elisabethville, *Symoens 12354* (K); *D. conferta* Ridl.–Malaysia, Borneo, Sepilok Forest Reserve, *Kadir A2744* (K),; *D. deremensis* Engl.—Tanzania, East Usambara Mountains, *Borhidi* et al. *87237* (K); *D. draco* L.- Madeira, *Mandon 245* (K); *D. ellenbeckiana* Engl.—Kenya, Northern Province, Sololo, Burroli Mt., *Glover & Samuel 3262* (K); *D. fragrans* (L.) Ker Gawl.—Equatorial Guinea, Fernando Po, Mioka area, *Boughey 96* (K); *D. mannii* Baker—Tanzania, Eastern Province, Kilosa District, *Semsei 1006* (K); *D. multiflora* Warb. ex P.Sarasin & Sarasin.—Philippines, Mindoro Paluan, *Ramos 39508* (K); *D. ombet* Kotschy & Peyr.—Sudan, Mt. Erkowit, *Schweinfurth 250* (K); Ethiopia, *Friss* et al. *10741* (K); *D. pendula* Peyr.–Malaysia, Telok Forest Reserve, Kepong, *Kochumenn 94847* (K); *D. reflexa* Lam.—Tanzania, Tanga District, *Greenway 8709* (K); *D. schizantha* Baker—Djibouti, Wadi Dounyar, S of Ali Sabieh, *Collenette 8644* (K); *D. serrulata* Baker—Saudi Arabia, South Hijag, between Abha and the Najran plateau, *Collenette 1291* (K); Yemen, south side of Sebel Minmar (Sadah-Sagayn), *Wood 624* (K); *D. surculosa* var. *surculosa* Lindl.—Nigeria, Benin Province, Okomu Forest Reserve, *Brenan* et al. *9027* (K).

Results

Morphological descriptions and interpretations

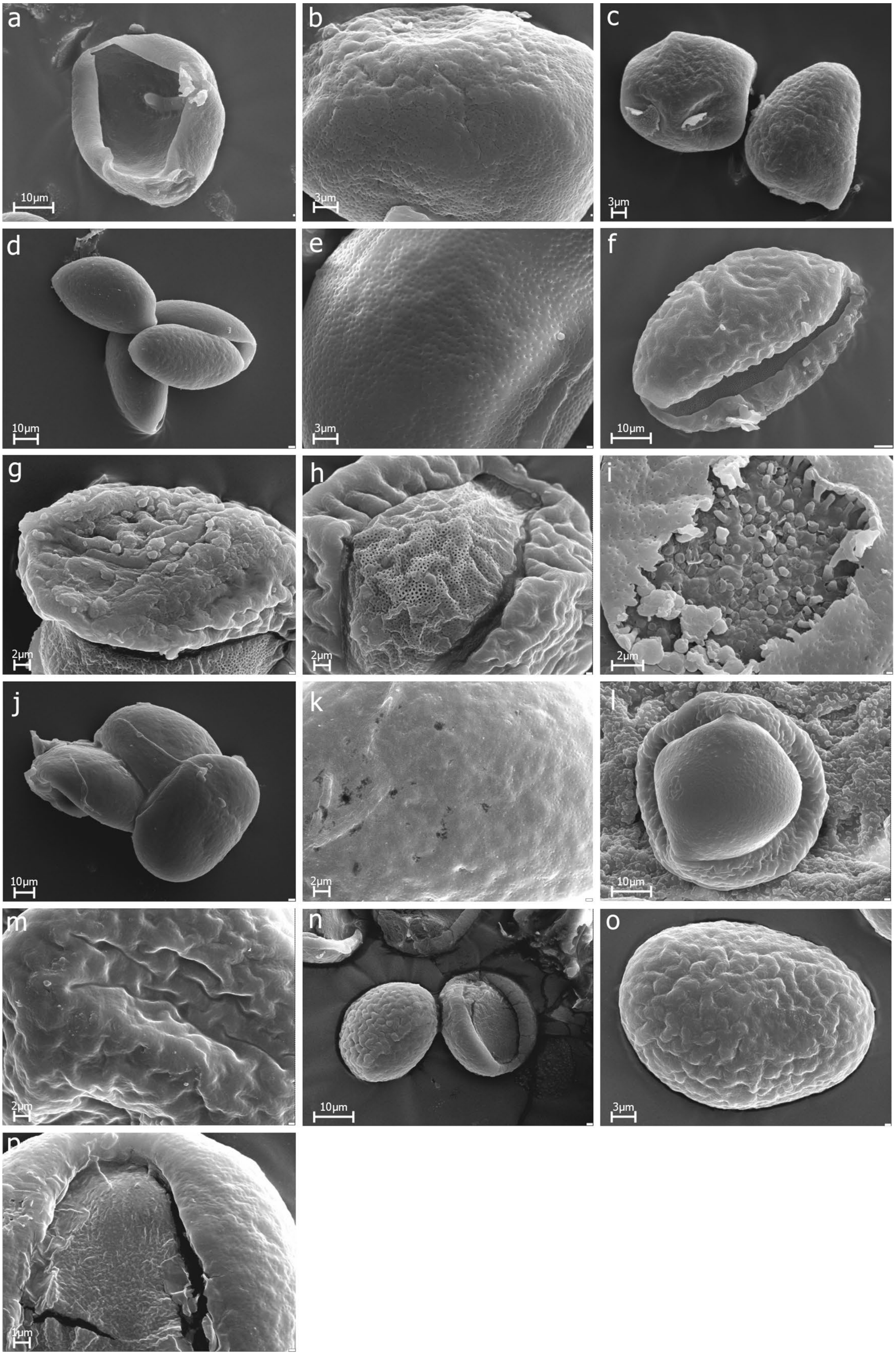
Chrysodracon

Pollen grains of *Chrysodracon* species are dispersed as monads, rarely as dyads, e.g., in *C. fernaldii* (Fig. 1c). Pollen grains are medium-sized (25–50 µm) and large (> 50 µm). The mean length of the long axis (LA) ranges from 51.8 in *C. fernaldii* to 60.2 µm in *C. aurea*, while the length of short axis (SA) ranges from 40.8 in *C. aurea* to 45.9 µm in *C. forbesii.* The outline is circular (Fig. 1a, d, g). The mean LA/SA ratio ranges from 1.19 in *C. fernaldii* to 1.53 in *C. aurea* (Table 1). Pollen shapes (based on LA/SA ratio) are subprolate (*C. fernaldii*) and prolate (*C. aurea* and *C. forbesii*), (Table 2). Exine ornamentation on the proximal surface is psilate-perforate in *C. aurea* (Fig. 1a, b), psilate-perforate and irregularly folded in C. *fernaldii* (Fig. 1d, e) and fossulate in *C. forbesii* (Fig. 1g, h). The aperture occupies nearly the entire distal hemisphere, and the proximal face is convex and the distal side is flatter (Fig. 1c) or convex (Fig. 1f, i). The monoulcerate pollen grains are bordered by a rim from the proximal hemisphere thin in *C. aurea* (Fig. 1c) and thick in *C. forbesii* (Fig. 1g, i, j). The germinal aperture of the pollen grains of *Chrysodracon* is variable in shape: circular (Fig. 1c) or oval (Fig. 1f, i). The apertural area in *C. aurea* is granulate (Fig. 1c), psilate-perforate-verrucate in *C. fernaldii* (Fig. 1f), while in *C. forbesii*, it is microreticulate (Fig. 1g, i), or psilate-perforate (Fig. 1j).

Dracaena

Pollen grains in species of *Dracaena* are found as monads, rarely as dyads, e.g., in *D. mannii*. They differ markedly in their dimensions. Pollen grains are medium-sized (25-50 µm) and large (> 50 µm). The mean length of the long axis (LA) ranges from 28.0 µm in *D. schizantha* to 74.6 µm in *D. pendula*, while the mean length of the short axis (SA) ranges from 21.0 µm in *D. schizantha* to 62.0 µm *in D. pendula* (Table 1). The outline in the equatorial view is elliptic and circular in the polar view. Pollen grains of *Dracaena* are bilaterally symmetrical. The basic shape of the pollen grains studied is subprolate and prolate (Table 2). In subprolate pollen grains, the mean LA/SA ratio ranged from 1.14 in *D. aletriformis* to 1.33 in *D. ellenbeckiana*, whereas in prolate pollen grains, the mean LA/SA ratio ranges from 1.35 in *D. mannii* and *D. schizantha* to 1.43 in *D. draco*.

The aperture of pollen grains is variable. The pollen grains possess a monosulcate aperture, which can extend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◂**Fig. 4** SEM micrographs of pollen grains of *Dracaena* species studied. **a-c** *Dracaena draco.* **a** In distal view. **b** Proximal surface. **c** Two pollen grains. **d, e** *Dracaena ellenbeckiana.* **d** In proximal and distal view. **e** Exine surface, enlargement of **d**. **f-i** *Dracaena fragrans.* **f** In lateral view**, g** In proximal view. **h, i** Distal surface. **j-m** *Dracaena mannii.* **j** In proximal view. **k** Exine surface, enlargement of **j**. **l** In distal view. **m** Surface of hemisphere rim. **n-p** *Dracaena multiflora.* **n** In proximal and distal view. **o** Proximal surface. **p** Distal surface

from one extremity of the pollen grain to the other (Figs. 2a, e, 3m, 4d, f, 5e, j) or be shorter (Figs. 2i, m, 3e, l, 4n, p, 5a, k, o). Sometimes it is narrow in the middle and wide at the ends (Figs. 2e, 3m, 4d, 5e). The margin of the sulcus in most species is straight (Figs. 2e, m, 3 l, 4a, d, 5e), slightly folded (Figs. 4p, 5j) or folded (Figs. 2a, j, 3b, 4i).

In *D. aubryana* (Fig. 3c)*, D. cambodiana* (Fig. 3d), *D. mannii* (Fig. 4l) and in *D. afromontana* and *D. arborea*, the aperture occupies nearly the entire distal hemisphere (ulcerate pollen). SEM observations (Table 2) showed that ornamentation of non-apertural areas is: microreticulate (Figs. 3m, n, 4b, c, 5b, h, i), fossulate (Figs. 2b, d, h, 4g, h, m, n, o) or psilate-perforate (Figs. 2e, k, l, 3a, d, g, h, j, k, 4e, j, k, 5c, d, m). The proximal surface in boat-shaped pollen possesses the same sculpturing as the distal surface. However, in *D. reflexa*, the central proximal side has a folded sculpturing (Fig. 5e), while the rest of the surface is psilate-fossulate (Fig. 5f). Our study shows that the aperture membranes (Table 2) are microreticulate (Figs. 2g, 4g, h, 5e, g), microreticulate-baculate (Fig. 3c), baculate (Fig. 3b, 4i), psilate-perforate (Figs. 2c, m, 3a, m, 4a, f, l, 5a, j) psilate-perforate-verrucate (Figs. 3i, 5l, o, p), and irregularly folded (Figs. 2j, 4p). Pollen grains in *D. aubryana* and *D. fragrans* have heterogeneous sculpturing on the apertural area (Figs. 3c, 4h, i). Irregular perforations on the proximal and distal surface are present, and the wall structure is tectate-columellate (Fig. 6).

Chrysodracon versus *Dracaena*

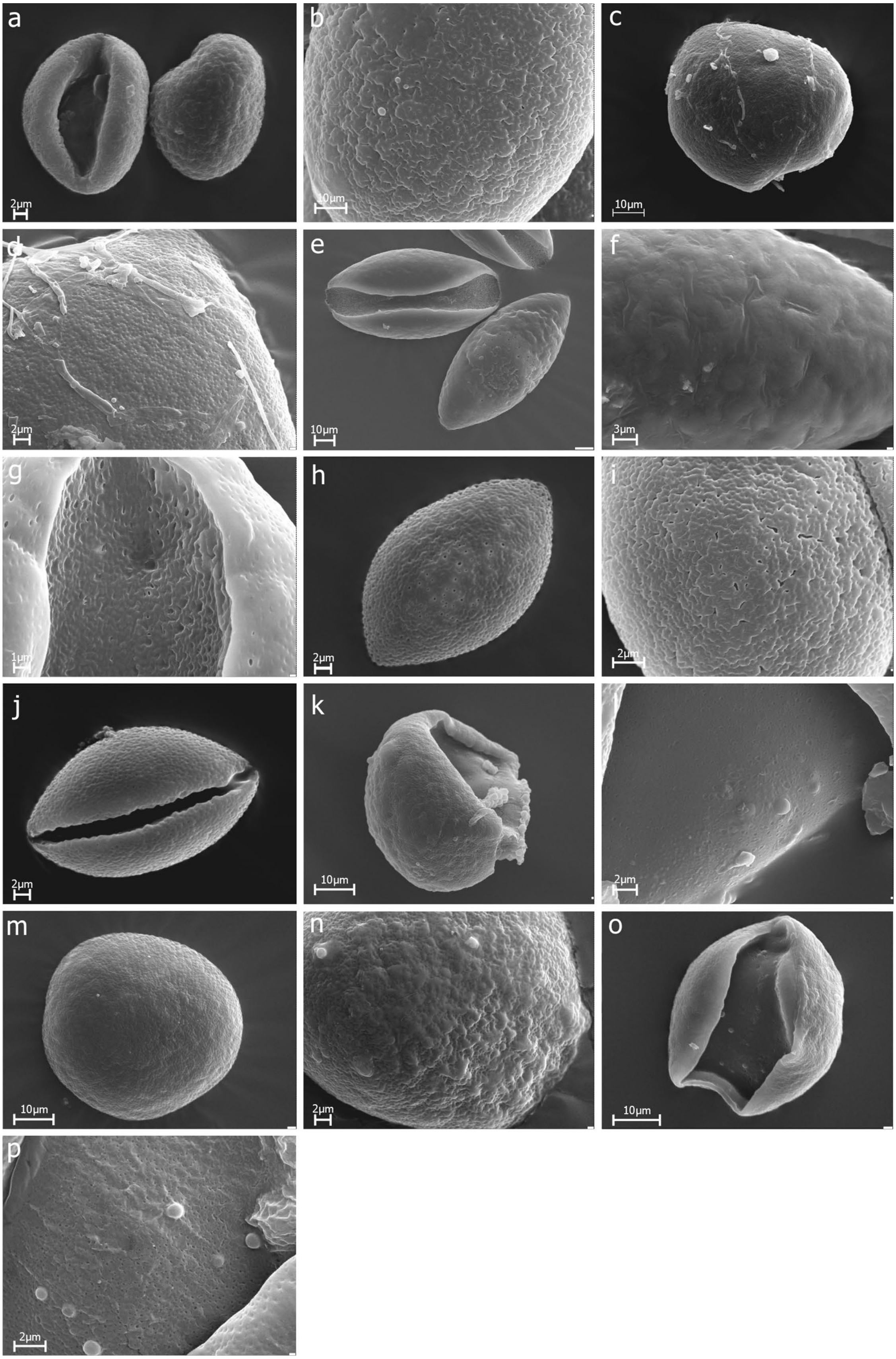
The comparison of quantitative features of pollen of *Chrysodracon* and *Dracaena* species according to the Tukey's tests ($P < 0.05$), the studied species formed eleven homogeneous groups for the LA, nine homogeneous groups for the SA characteristic and five groups for LA/SA (Fig. 7). In the case of LA/SA, homogeneous groups were considerably more overlapped as compared to LA and SA. Species of *Chrysodracon* genus did not form a distinct group in any of studied characteristics. Based on LA and SA, two groups of species from *Dracaena* genus can be clearly distinguished: *D. schizanta*, *D. ombet*, *D. americana* and *D. serrulata*, *D. cambodiana*, *D. draco*.

Discussion

Our study show distinctive variation in pollen grains morphology of the *Dracaena* and *Chrysodracon* genera. Pollen grains in most species of both genera are found as monads rarely as dyads. Ojeda et al. (1984) showed dyads and tetrads in *D. americana*. Pollen grains of *Dracaena* are large and medium-sized. Among the examined species, the biggest pollen was found in *D. pendula* and the smallest pollen was reported in *Dracaena* species from the "dragon tree group" (*D. afromontana, D. americana, D. cambodiana, D. draco, D. ellenbeckiana, D. ombet, D. schizantha* and *D. serrulata*). In comparison with the study of Ojeda et al. (1984), the recorded dimensions of the pollen grains in *D. americana* and *D. fragrans* are smaller. In the former species, they are 30.4 × 22.9 µm (versus 36.9 × 23.9 µm in the cited work), while in the latter species, it is 50.1 × 38.1 µm (versus 67.8 × 48 µm). The pollen grain dimensions of *D. cambodiana* were reported to be 28.32 × 19.68 µm (Guang-Zheng 1993). Based on the findings in this study, they may be bigger, attaining 36.4 x 27.3 µm.

Our observations confirmed earlier studies (Erdtman 1952; Ojeda et al. 1984; Ojeda and Ludlow-Wiechers 1995; Bos 1998; Rudall et al. 2000; Mwachala 2005; Patil and Pai 2011) reporting pollen grains in the genus *Dracaena* as monosulcate. In five species of *Dracaena*: *D. afromontana, D. arborea, D. aubryana, D. cambodiana* and *D. mannii*, pollen is dimorphic, composed of mixed monoulcerate and monosulcate grains. Furness and Rudall (2001) reported that in the order Asparagales, two different types of apertures are present. The appearance of the sulcus in many monocot pollen grains and the shape of the grains itself varies considerably with the respective pollen configuration. The sulcus form types may be important taxonomic characters in some families (Halbritter and Hesse 1993). Monosulcate pollen is considered to be a plesiomorphic feature in monocots and basal angiosperms (Sampson 2000; Furness and Rudall 1999, 2000, 2001). However, some authors express caution when referring to its basal character (Penet et al. 2005). A single aperture at the distal pole characterizes gymnosperm taxa of higher rank, i.e. Cycadopsida, Bennettitopsida and Ginkgopsida (Erdtman 1965; Tekleva et al. 2007; Zavialova et al. 2011; Korszun and Klimko 2014).

The exine microsculpture of the pollen grains of *Dracaena* and *Chrysodracon* species provides diagnostic features of systematic importance. Ornamentation is not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◂**Fig. 5** SEM micrographs of pollen grains of *Dracaena* species studied. **a, b** *Dracaena ombet.* **a** In proximal and distal view. **b** Exine surface, enlargement of **a**. **c, d** *Dracaena pendula.* **c** In proximal view. **d** Exine surface, enlargement of **c**. **e–g** *Dracaena reflexa.* **e** In proximal and distal view. **f** Proximal surface. **g** Distal surface. **h-j** *Dracaena schizantha.* **h** In proximal view. **i** Exine surface, enlargement of **h**. **j** In distal view. **k, l** *Dracaena serrulata.* **k** In lateral view. **l** Distal surface. **m-p** *Dracaena surculosa* var. *surculosa.* **m** In proximal view. **n** Exine surface, enlargement of **m**. **o** In distal view. **p** Exine surface, enlargement of **o**

uniform all over the pollen grains, but differs between the proximal face and distal pollen regions in studied species. On the proximal surface of the pollen grains, three basic types of the exine sculpturing were distinguished in our study. Also, large differences of the exine sculpture were observed on the apertural area. The exine surface of pollen grains in eight species of *Dracaena* in China was studied by Guang-Zheng (1993). That author described three types of pollen exine sculpture: foveolate (*D. cochinchinensis* (Lour.) S.C. Chen and *D. menglaensis* G. Z. Ye), rugulate (*D. cambodiana* and *D. terniflora* Roxb.), reticulate (*D. gracilis* Wall. ex Baker, *D. angustifolia* Roxb. and *D. ensifolia* Wall.) on the proximal side. Ojeda et al. (1984) concluded that the proximal surface of boat-shaped pollen grains in *D. americana* was psilate-perforate, while in *D. fragrans* it was fossulate. In our study, we did not observe in *D. cambodiana* and *D. americana* pollen grains like those described above. The sculpturing of the sulcus exine on pollen grains was presented only by Ojeda et al. (1984) in *D. fragrans*, who described them as microverrucate, while in our study, we observe microreticulate and baculate. The sulcus features and the sulcus membranes are a potential useful systematic character for some of *Dracaena* examined species. The wall structure was previously examined in *Dracaena* by Meier and Yaroshevskaya (1973). They concluded that the wall structure was tectate-columellate. Our results are consistent with the descriptions given by those authors. From the palynological point of view, the pollen grains of the examined species of *Chrysodracon* significantly differ from the most

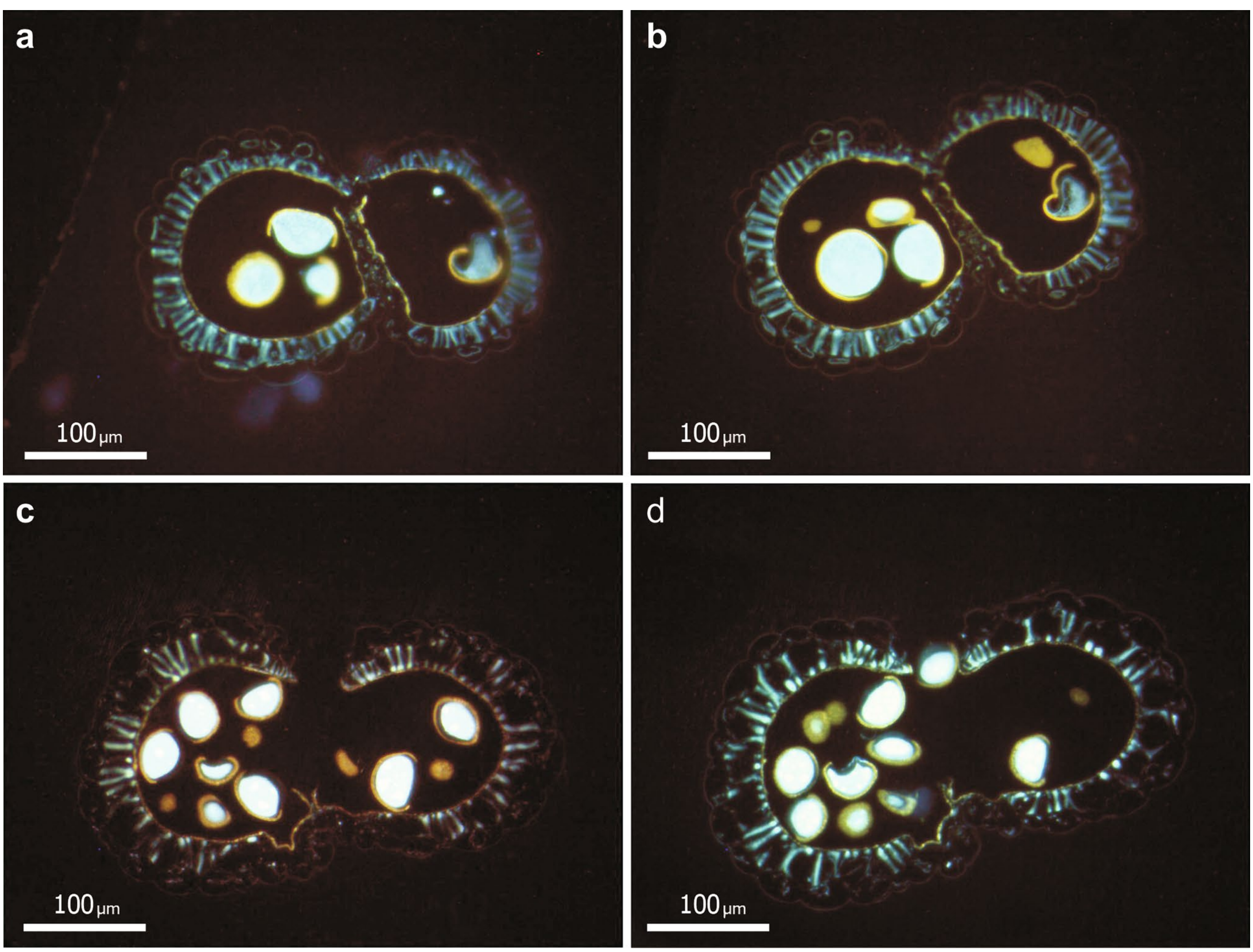

Fig. 6 FM micrographs of exine structure in *Dracaena*: **a, b** *D. aubrayna,* **c**, **d** *D. reflexa*

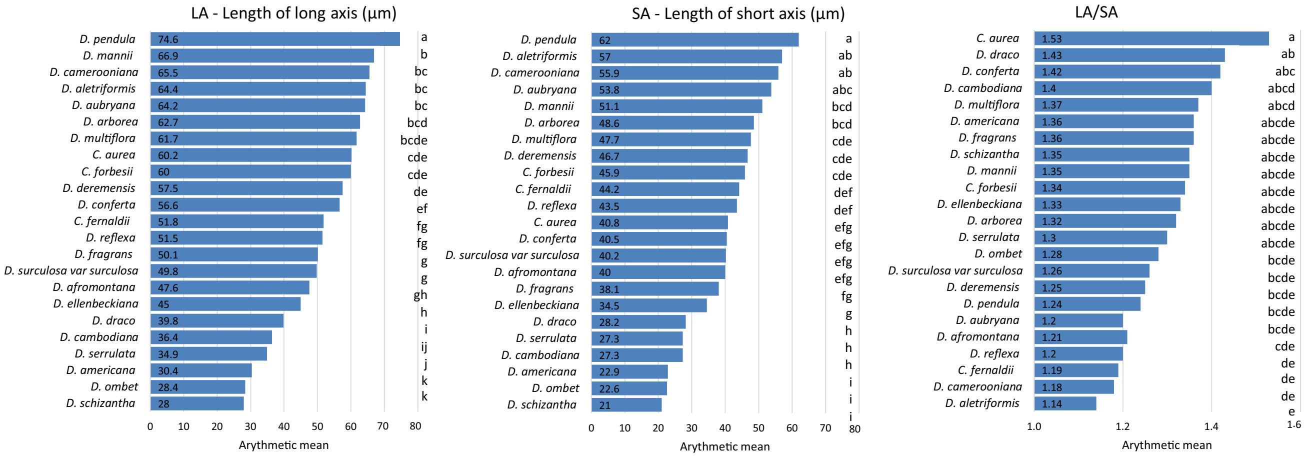

Fig. 7 Arithmetic means and results of Tukey's tests for quantitative characteristics of pollen grains in *Chrysodracon* and *Dracaena*. Species denoted by the same letter (s) do not differ significantly at P < 0.05

species of *Dracaena* in apertures type, but are very similar to pollen grains of *Sansevieria* (Ojeda et al. 1984, Klimko et al. 2017).

Conclusions

1. The pollen grains from the *Chrysodracon* and *Dracaena* genera assessed in terms of their size are classified as medium and large. Their shape is defined as subprolate, prolate or prolate-spheroidal. Based on pollen size and shape, it is not possible to distinguish these two genera.
2. The pollen grains of *Chysodracon* are monoulcerate whereas in *Dracaena*–monosulcate and monoulcerate.
3. Exine ornamentation is not uniform all over the pollen grain but differs between proximal face and distal region.
4. The results of investigations of the exine sculpture in pollen grains can be used in taxonomy of species from *Chrysodracon* and *Dracaena* genera.

A more extensive study of pollen morphology for all dracenoid genera will provide a more comprehensive understanding of systematic relations between their species.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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