

Palynomorphological peculiarities of representatives of tribes *Lindenbergieae* and *Cymbarieae* and pollen evolution in early-branching lineages of *Orobanchaceae*

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Abstract. Pollen morphology of four species belonging to four genera of the tribe *Cymbarieae* and two species of *Lindenbergia* of the tribe *Lindenbergieae* (*Orobanchaceae*) was studied using light and scanning electron microscopy. Pollen grains in *Lindenbergieae* are 3-colporate (rarely 2-colporate), prolate, spheroidal and oblate-spheroidal, small-sized, with reticulate exine sculpture. Pollen grains in *Cymbarieae* are 3-colpate, rarely 4-colpate, prolate, spheroidal and oblate-spheroidal, medium-sized. Exine sculpture in *Cymbarieae* is retipilate and rugulate-retipilate. Pollen characters of *Cymbarieae* and *Lindenbergieae* are compared with pollen patterns in *Paulowniaceae* and crown clades of *Orobanchaceae*. The earliest-branching clade of *Orobanchaceae* (*Lindenbergieae*) is palynomorphologically similar to *Paulowniaceae* (the clade sister to all *Orobanchaceae*) and to *Wightia*. These palynomorphological findings confirm the phylogenetic patterns recently revealed in basal *Orobanchaceae* and their closest relatives. It is concluded that the colporate (most probably 3-colporate) type of pollen grains could be ancestral in *Orobanchaceae*. Pollen diversity in crown clades of *Orobanchaceae* evolved on the base of a few pollen types and subtypes, which were peculiar to hypothetical ancestors of *Orobanchaceae* and are probably preserved in the extant taxa of *Paulowniaceae* and *Lindenbergieae*.

Keywords: *Cymbarieae*, *Lindenbergieae*, *Orobanchaceae*, pollen evolution, pollen morphology, phylogeny, taxonomy

Introduction

The tribe *Cymbarieae* D. Don (*Orobanchaceae* Vent.) in its current circumscription includes six or seven genera and ca. 14 species of root hemiparasites (Fischer, 2004; Bennett, Mathews, 2006; Reveal, 2012; McNeal et al., 2013; Olmstead, 2016). The genera currently included in the tribe are *Bungea* C.A. Mey. (2 species, southwestern and Central Asia and China), *Cymbaria* L. sensu lato (4 species, southeastern Europe, Central and eastern Asia; many authors also include here *Cymbochasma* (Endl.) Klokov & Zoz), *Lesquereuxia* Boiss. (1 species, *L. syriaca* Boiss. & Reut. = *Siphonostegia syriaca* (Boiss. & Reut.) Boiss., Eastern Mediterranean; most probably nested in *Siphonostegia*: see McNeal et al., 2013), *Monochasma* Maxim. ex Franch. & Sav. (4 species, East Asia), *Schwalbea* L. (1 species, *S. americana* L., eastern North America), and *Siphonostegia* Benth. (2 species: *S. chinensis* Benth. and *S. laeta* S. Moore, East Asia; or 3 species, if *S. syriaca* is included) (Fischer, 2004; Bennett, Mathews, 2006; Takhtajan, 2009; McNeal et al., 2013; Olmstead, 2016).

The genus *Lindenbergia* Lehm. is represented by non-parasitic taxa and includes 12–15 species occurring mostly in tropical regions, from northeastern Africa through southern and southeastern Asia (including the Himalayas) to Philippines (Mabberley, 1997; Stevens, 2001–onwards; Fischer, 2004; Olmstead, 2016).

In earlier variants of the system of A.L. Takhtajan (1987, 1997) the mentioned genera *Schwalbea*, *Bungea*, *Siphonostegia*, *Cymbaria*, and *Monochasma* were included (with many other genera) in the tribe *Rhinanthoeae* Lam. & DC. of *Scrophulariaceae* subfam. *Rhinanthoideae*. In the latest version of his system, Takhtajan (2009) placed the genera *Schwalbea*, *Cymbaria* (including *Cymbochasma*), *Siphonostegia*, *Lesquereuxia*, *Bungea*, *Monochasma* in the tribe *Cymbarieae* (also with some other genera), and their familial and subfamilial placement remained the same. Fischer (2004) included in *Cymbarieae* six genera: *Schwalbea*, *Cymbaria* (including *Cymbochasma*), *Siphonostegia*, *Lesquereuxia*, *Bungea*, and *Monochasma*.

Takhtajan (1987, 1997) initially placed *Lindenbergia* in *Scrophulariaceae* subfam. *Scrophularioideae* trib. *Gratiroleae* Benth. In 2009 he moved that genus to the

tribe *Stemodieae* Reveal, which was positioned in his system close to *Gratiroleae*, in the same subfamily. Fischer (2004) placed *Lindenbergia* in *Scrophulariaceae* trib. *Stemodieae*. Now the genus is placed in *Orobanchaceae* trib. *Lindenbergieae* T. Yamaz. (= *Lindenbergiaceae* Doweld, 2001).

Many authors studied and discussed pollen morphology of representatives of *Scrophulariaceae* and *Orobanchaceae* in general (Minkin, Eshbaugh, 1989), or specifically *Rhinantheae* (Inceoğlu, 1982; Lu et al., 2007; Tsymbalyuk, Mosyakin, 2017), and its taxonomic and evolutionary significance (see also Tsymbalyuk, Mosyakin, 2013a, b; Mosyakin, Tsymbalyuk, 2015a, b, 2017 and references therein). However, there are only a few publications reporting data on pollen of taxa now placed in *Cymbarieae*; these publications provide some data based on light and scanning electron microscopy (Inceoğlu, 1982; Minkin, Eshbaugh, 1989; Lu et al., 2007). Pollen grains of two species (*Bungea trifida* and *Lesquereuxia syriaca*) currently placed in *Cymbarieae* were also studied using transmission electron microscopy (Inceoğlu, 1982). However, no comprehensive analysis of palynomorphological peculiarities of *Cymbarieae* in its updated phylogeny-based circumscription has been done until now.

Prijanto (1969) provided the following information about pollen grains of *Lindenbergia*: "Pollen grains small, 3-colporate, rarely 2-colporate, oblate spheroidal to prolate spheroidal (polar axis 12–19 µm long, equatorial diameter 13–18 µm; apocolpium diameter 3–5 µm; exine about 0.8–1.5 µm thick, sexine as thick as nexine, reticulate". However, no images of pollen grains were published by Prijanto (1969). Hjertson (1995) updated the information of Prijanto (1969) and provided SEM images of pollen grains of *L. muraria* (Roxb. ex D. Don) Brühl and *L. grandiflora* (Buch.-Ham. ex D. Don) Benth. He concluded that "pollen grains in *Lindenbergia* are tricolporate, oblate to prolate in shape, with a 12–19 µm long polar axis and an equatorial diameter of 13–18 µm. The exine as well as the sexine is about 1 µm thick, and the surface is reticulate".

Molecular phylogenetic evidence indicate that *Cymbarieae* is one of the early-branching (basal) lineages of *Orobanchaceae*, most probably its second-branching clade, following the basalmost clade of *Lindenbergia* (*Orobanchaceae* trib. *Lindenbergieae* = *Lindenbergiaceae*) (McNeal et al., 2013; Cusimano, Wicke, 2016; Schneider et al., 2016; Schneider, Moore, 2017, etc.). According to molecular phylogenetic

studies (Bennett, Mathews, 2006; McNeal et al., 2013), the clade of *Cymbarieae* is subdivided into two subclades: one of these clades includes *Bungea*, *Cymbaria* (including *Cymbochasma*), and *Monochasma*; the other houses *Siphonostegia* (including *Lesquereuxia*) and *Schwalbea*.

Our earlier studies and analysis of pollen morphology in basal clades of *Scrophulariaceae* sensu stricto allowed us to outline the main trends of morphological pollen evolution in the family in its new circumscription and to hypothesize on possible ancestral pollen types in the group (Mosyakin, Tsymbalyuk, 2015, 2017). Because of that, we may expect that a comprehensive analysis of pollen morphology in early-branching clades of *Orobanchaceae* could bring comparable results and shed light on main trends of pollen evolution in that group as well.

The purpose of the present research was to study and analyze the morphological features of pollen grains of representatives of *Cymbarieae* and *Lindenbergieae* in the updated taxonomic circumscriptions of these tribes, and to compare the pollen patterns with existing systems and molecular phylogenetic data.

Materials and methods

Pollen of four species belonging to four genera of *Cymbarieae* (*Bungea*, *Cymbaria*, *Cymbochasma*, and *Siphonostegia*) was sampled in the National Herbarium of Ukraine (KW – herbarium of the M.G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, Kyiv, Ukraine). Pollen grains of two species of *Lindenbergia* were sampled in the herbarium of the Missouri Botanical Garden (MO; St. Louis, Missouri, USA). Data of the studied specimens are cited exactly according to the label information, in English translation and in original languages.

In general, the methods used in the present study are essentially the same as those we used earlier (see Mosyakin, Tsymbalyuk, 2015a, b, 2017). Pollen morphology was studied using light microscopy and scanning electron microscopy. For light microscopy studies (LM, Biolar, × 700), the pollen was acetolyzed following Erdtman (1952). For size determinations, 20 measurements were taken along the polar (P) and equatorial (E) 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 and investigated at the Center of Electron Microscopy of the

M.G. Kholodny Institute of Botany. The micrographs were minimally edited with Adobe Photoshop 6.0 to enhance the images.

Terminology used in descriptions of pollen grains mainly follows the glossaries by Tokarev (2002) and Punt et al. (2007) with some necessary minor adjustments.

General description of pollen grains

Lindenbergieae

Pollen grains in monads, radially symmetrical, isopolar, 3-colporate (rarely 2-colporate, according to Prijanto, 1969), prolate, spheroidal or oblate-spheroidal; mainly small-sized: P = 13.3–18.6 μm (12–19 μm , according to Prijanto, 1969), E = 13.3–18.6 μm . Outline in polar view 3-lobate, in equatorial view elliptical or circular. Colpi long, narrow, 1.3–2.7 μm wide, with mainly indistinct (sometimes distinct) more or less strict margins, with acute ends. Endoapertures mainly indistinct, circular, 2.4–2.7 μm long and wide. Exine 0.7–1.6 μm . Tectum nearly equal to infratectum. Columellae indistinct or distinct, thin, or exine layers invisible. Exine sculpture reticulate. Colpus membrane smooth.

Cymbarieae

Pollen grains in monads, radially symmetrical, isopolar, mainly 3-colpate, rarely 4-colpate, prolate, spheroidal, or oblate-spheroidal. The outlines in equatorial view elliptical or circular, in polar view sub-circular, circular, and sub-triangular; medium- or large-sized: P = 22.6–47.9 μm (up to 50 μm , according to Lu et al., 2007), E = 25.3–43.9 μm . Colpi long or medium-length, narrow, medium-width to wide, 1.3–6.6 μm wide, with indistinct, uneven margins, and blunt, acute, or indistinct ends. Exine 0.7–3.3 μm . Tectum nearly equal to infratectum, columellae mainly indistinct or thin and arranged more or less regularly. Exine sculpture retipilate, rarely rugulate-retipilate. Capita (pila heads) arranged in circle in most or all regions of pollen surface. Caput of pila 0.16–0.67 μm (up to 0.90 μm , according to Lu et al., 2007). Colpus membrane granulate.

Pollen types and subtypes

Based on their aperture types, pollen grains of the studied species belong to the same basic pollen types. The second type (3-colpate) contains four subtypes segregated according to their exine sculpture, pollen size, details of colpi, and thickness of the exine.

Type I — 3-colporate

Sculpture reticulate.

P = 13.3–18.6 μm , E = 13.3–18.6 μm .

Colpi long, narrow, 1.3–2.7 μm wide, with acute ends.

Endoapertures mainly indistinct, circular, 2.4–2.7 μm long and wide.

Exine 0.7–1.6 μm . *Lindenbergia philippensis*, *L. sinaica*.

Type II — 3-colpate

Subtype 1. Sculpture retipilate. Caput of pila 0.17–0.33 μm .

P = 38.6–47.9 μm , E = 34.6–43.9 μm .

Colpi long, medium-width, 2.4–3.3 μm wide, ends acute.

Exine 1.3–3.3 μm . *Bungea trifida*.

Subtype 2. Sculpture retipilate and rugulate-retipilate. Caput of pila 0.41–0.67 μm .

P = 37.2–47.9 μm , E = 33.2–42.6 μm .

Colpi medium-length, wide, 4.0–6.6 μm wide, ends blunt, sometimes acute.

Exine 1.6–2.7 μm . *Cymbaria dahurica*.

Subtype 3. Sculpture retipilate. Caput of pila 0.17–0.25 μm .

P = 29.3–33.2 μm , E = 30.6–35.9 μm .

Colpi medium-length, medium-width, 2.7–5.3 μm wide, ends blunt, indistinct.

Exine 0.7–1.3 μm . *Cymbochasma borysthena*.

Subtype 4. Sculpture retipilate. Caput of pila 0.16–0.25 μm .

P = 22.6–29.3 μm , E = 25.3–29.3 μm .

Colpi long, narrow, 1.3–2.4 μm wide, ends blunt.

Exine 1.3–2.4 μm . *Siphonostegia chinensis*.

Descriptions of pollen grains

Genus *Lindenbergia* Lehm.

Lindenbergia philippensis (Cham.) Benth. (Fig. 1, a–c; Fig. 4, a–d)

LM. Pollen grains 3-colporate, oblate-spheroidal and spheroidal, occasionally prolate, in polar view 3-lobate, in equatorial view elliptical and circular. P = 13.3–17.3 μm , E = 14.6–18.6 μm . Colpi long, narrow, 1.3–2.7 μm wide, with indistinct (some distinct) more or less strict margins, tapering to acute ends; colpus membrane smooth. Endoapertures indistinct, circular, 2.4–2.7 μm wide, 2.4–2.7 μm long. Mesocolpium = 9.3–10.6 μm , apocolpium = 2.7–4.0 (5.3) μm . Exine 1.1–1.6 μm thick. Tectum nearly equal to infratectum. Columellae indistinct or distinct, thin. Exine sculpture indistinct or distinct, microreticulate.

SEM. Sculpture reticulate. Colpus membrane smooth.

Specimen investigated: Philippines; Mountain Province; Bontoc Municipality; Bontoc territory; Caluttit; 17°05' N, 120°58' E; 1000 m elev. 17 November 1982. C.C. Bodner. No 131 (MO).

***Lindenbergia sinaica* Benth.** (Fig. 1, *d–f*; Fig. 4, *e–h*)

LM. Pollen grains 3-colporate, prolate and occasionally spheroidal, occasionally oblate-spheroidal, in polar view 3-lobate, in equatorial view elliptical and circular. $P = 14.6–18.6 \mu\text{m}$, $E = 13.3–17.3 \mu\text{m}$. Colpi long, narrow, 2.0–2.4 μm wide, with indistinct (occasionally some distinct) more or less strict margins, tapering to acute ends; colpus membrane smooth. Endoapertures indistinct, more or less circular, 2.7 μm wide, 2.4–2.7 μm long. Mesocolpium = 7.9–10.6 μm , apocolpium = 4.0 μm . Exine 0.7–1.1 μm thick, exine layers invisible. Exine sculpture indistinct, foveolate.

SEM. Sculpture reticulate. Colpus membrane smooth.

Specimen investigated: [Ethiopia]. About 150 km SW of Assab [Eritrea], along road to Kombolcha [Ethiopia]. Alt.: 400 m. Dry, rocky slope. 18.I 1966. W. de Wilde. No 9771 (MO).

Genus *Bungea* C.A. Mey.

***Bungea trifida* (Vahl) C.A. Mey.** (Fig. 2, *a–c*; Fig. 5, *a–d*)

LM. Pollen grains 3-colpate, prolate and occasionally spheroidal, in polar view sub-triangular and/or circular, in equatorial view elliptical and circular. $P = 38.6–47.9 \mu\text{m}$, $E = 34.6–43.9 \mu\text{m}$. Colpi long, medium-width, 2.4–3.3 μm wide, with indistinct, uneven margins, tapering to more or less acute or indistinct ends; colpus membrane granulate. Mesocolpium = 26.6–34.6 μm , apocolpium = 6.6–13.3 μm . Exine 1.3–3.3 μm thick. Tectum nearly equal to infratectum. Columellae invisible. Exine sculpture indistinct, microreticulate.

SEM. Sculpture retipilate. Caput of pila 0.17–0.33 μm . Colpus membrane granulate.

Specimens investigated: 1. Armenian SSR [now Armenia], Vēdi District [now in Ararat Province], right slope of the Vēdi River, between Azizkend and Daynaz villages, phrygana. 27.V 1960. A. Takhtajan, E. Gabrielian, L.I. Mulkijanian (KW) [Label in Russian: Арм. ССР, Вединский р-н, правый борт р. Веди, с.с. Азизкенд × Дайназ, фригана. 27.V 1960. А. Тахтаджян, Э. Габриелян, Л.И. Мулкиджанян]. 2. Turkey. B 10 Kars: Pamuk Dağ, 20 km from Iğdir to

Doğubayazit. 1600 m. Pastures. Perennial. Flower flava [sic!]. 30 May 1966. Davis, No 43867 (KW).

Genus *Cymbaria* L.

***Cymbaria dahurica* L.** (Fig. 2, *d–f*; Fig. 5, *e–h*)

LM. Pollen grains 3-colpate, prolate and occasionally oblate-spheroidal, in polar view sub-triangular, in equatorial view elliptical. $P = 37.2–47.9 \mu\text{m}$, $E = 33.2–42.6 \mu\text{m}$. Colpi medium-length, 4.0–6.6 μm wide, with indistinct, uneven margins, tapering to blunt, sometimes acute ends, colpus membrane smooth and granulate. Mesocolpium = 26.6–33.2 μm , apocolpium = 10.6–19.9 μm . Exine 1.6–2.7 μm thick. Tectum nearly equal to infratectum. Columellae indistinct. Exine sculpture indistinct, sometimes distinct, microreticulate.

SEM. Sculpture retipilate and rugulate-retipilate. Caput of pila 0.41–0.67 μm . Colpus membrane granulate.

Specimens investigated: 1. Khakassian Autonomous Region [now Republic of Khakassia, Russian Federation], Altai District, near Ochury village. Southern rocky slope, fine-turfgrass steppe. 30 June 1969. A. Koroleva (KW) [Label in Russian: Хакасская авт. обл., Алтайский р-н, окр. с. Очуры. Южный каменистый склон, мелко-дерновинная степь. 30.VI 1969. А. Королева]. 2. Transbaikalia [now Zabaysky Krai, Russian Federation]. On dry mountain slopes and in steppes near Nerchinsk, abundant. June 1898. Coll. Gubelman and Migunov (KW) [Label in Russian: Забайкалье. На сухих склонах гор и в степях около Нерчинска в изобилии. Июнь 1898; Собр. Губельман и Мигунов].

Genus *Cymbochasma* (Endl.) Klokov & Zoz

***Cymbochasma borysthena* (Pall. ex Schlecht.) Klokov & Zoz** (*Cymbaria borysthena* Pall. ex Schlecht.) (Fig. 3, *a–c*; Fig. 5, *i–l*)

LM. Pollen grains 3-colpate, occasionally 4-colpate, oblate-spheroidal, in polar view sub-circular, in equatorial view elliptical. $P = 29.3–33.2 \mu\text{m}$, $E = 30.6–35.9 \mu\text{m}$. Colpi medium-length, medium-width, 2.7–5.3 μm wide, with indistinct, uneven margins, tapering to blunt, indistinct ends, colpus membrane smooth and granulate. Mesocolpium = 22.6–26.6 μm , apocolpium = 6.6–9.3 μm . Exine 0.7–1.3 μm thick. Tectum nearly equal to infratectum. Columellae indistinct. Exine sculpture indistinct, sometimes distinct, microreticulate.

SEM. Sculpture retipilate. Caput of pila 0.17–0.25 μm . Colpus membrane granulate.

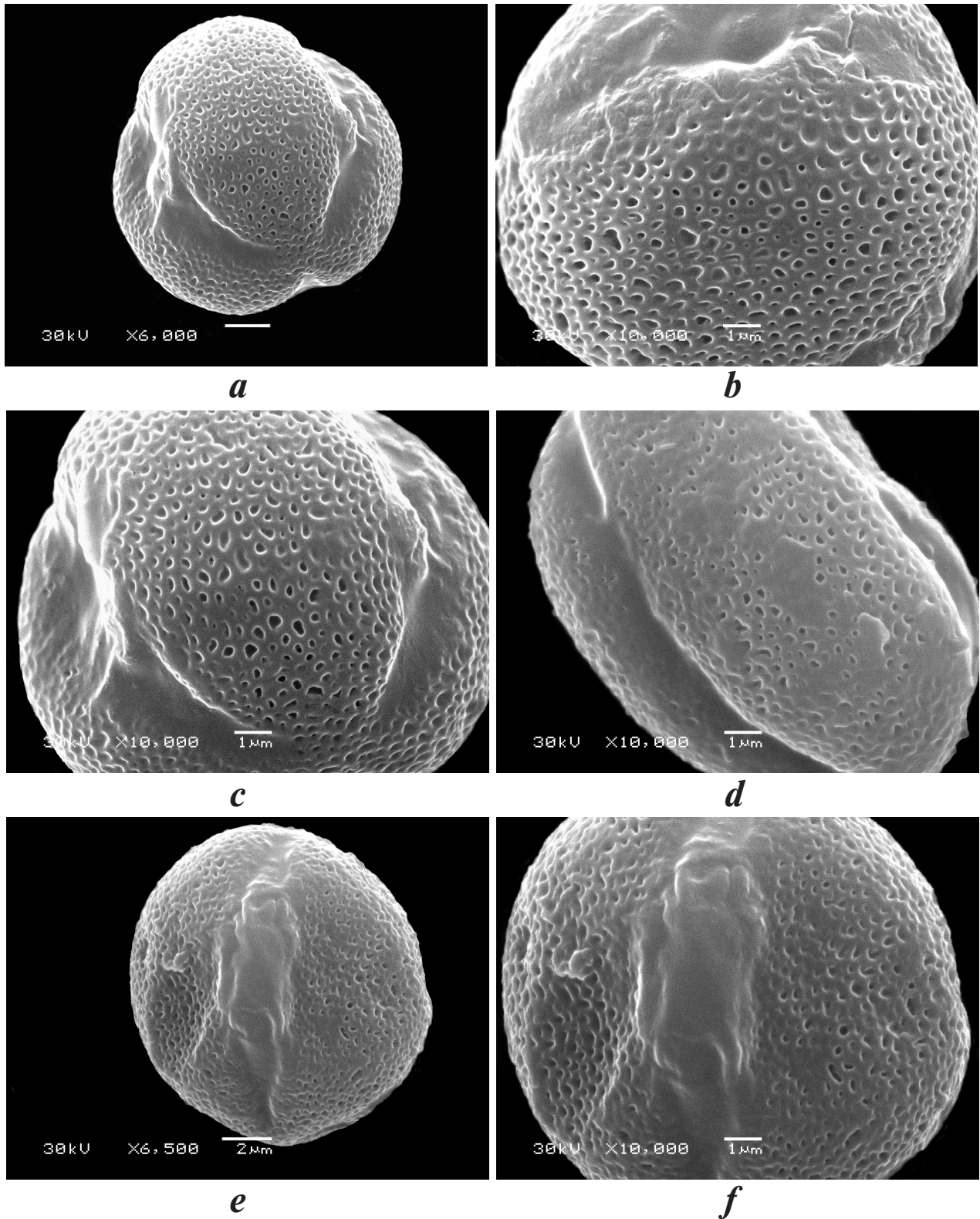
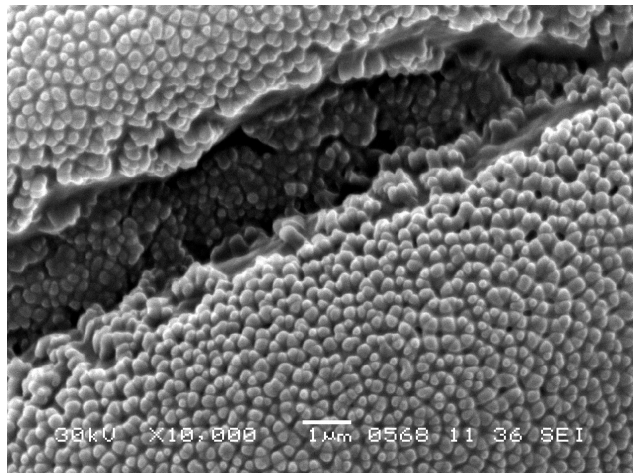


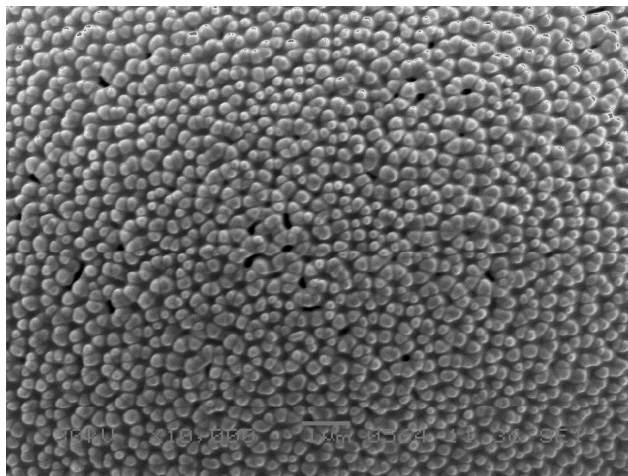
Fig. 1. Pollen grains of *Lindenbergia* (scanning electron microscopy): *a–c* – *L. philippensis*; *d–f* – *L. sinaica*; *a* – polar and equatorial view; *e* – equatorial view; *b–d, f* – reticulate exine sculpture



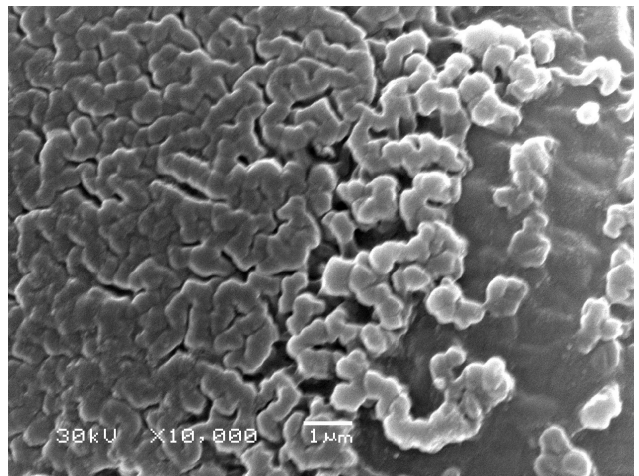
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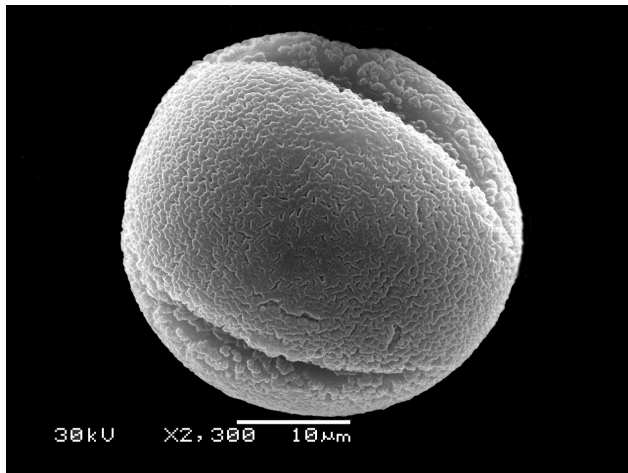
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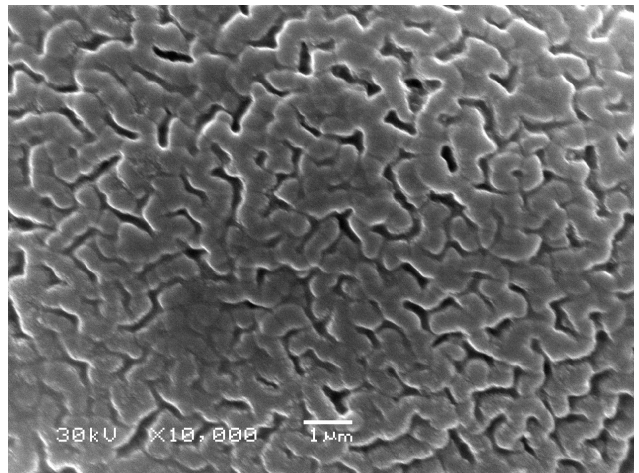
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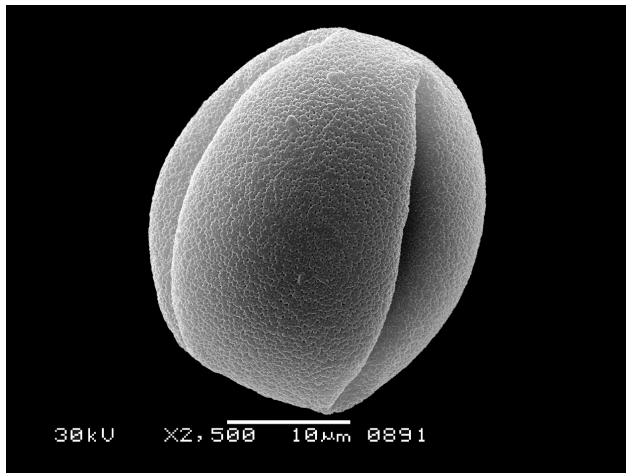


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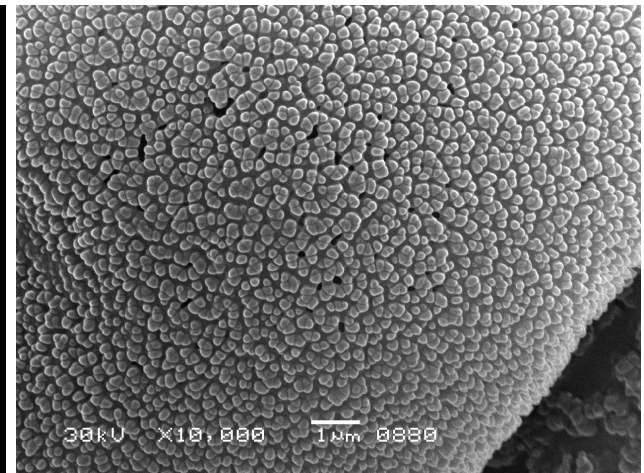


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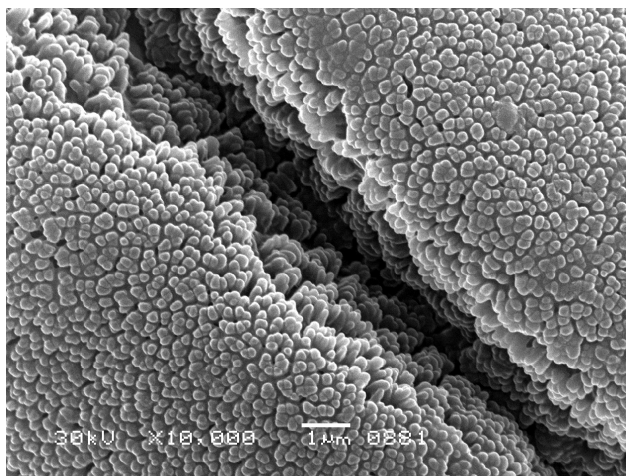
Fig. 2. Pollen grains of *Bungea* and *Cymbaria* (scanning electron microscopy): *a–c* – *B. trifida*; *d–f* – *C. dahurica*; *a, e* – equatorial view; *b, c* – retipilate exine sculpture; *d, f* – rugulate-retipilate exine sculpture



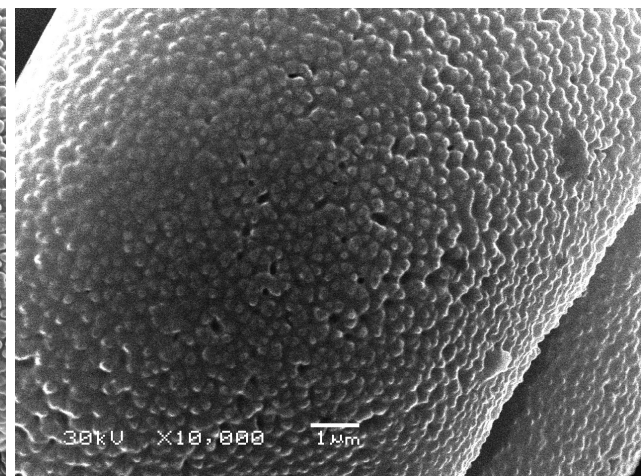
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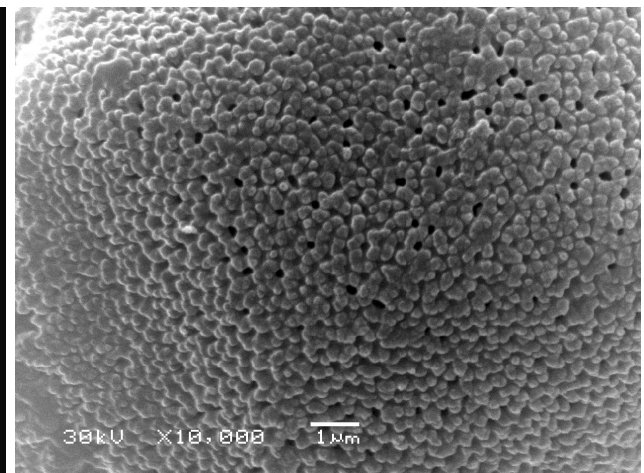
c



d



e



f

Fig. 3. Pollen grains of *Cymbochasma* and *Siphonostegia* (scanning electron microscopy): *a–c* – *C. borysthena*; *d–f* – *S. chinensis*; *a, e* – equatorial view; *b–d, f* – retipilate exine sculpture

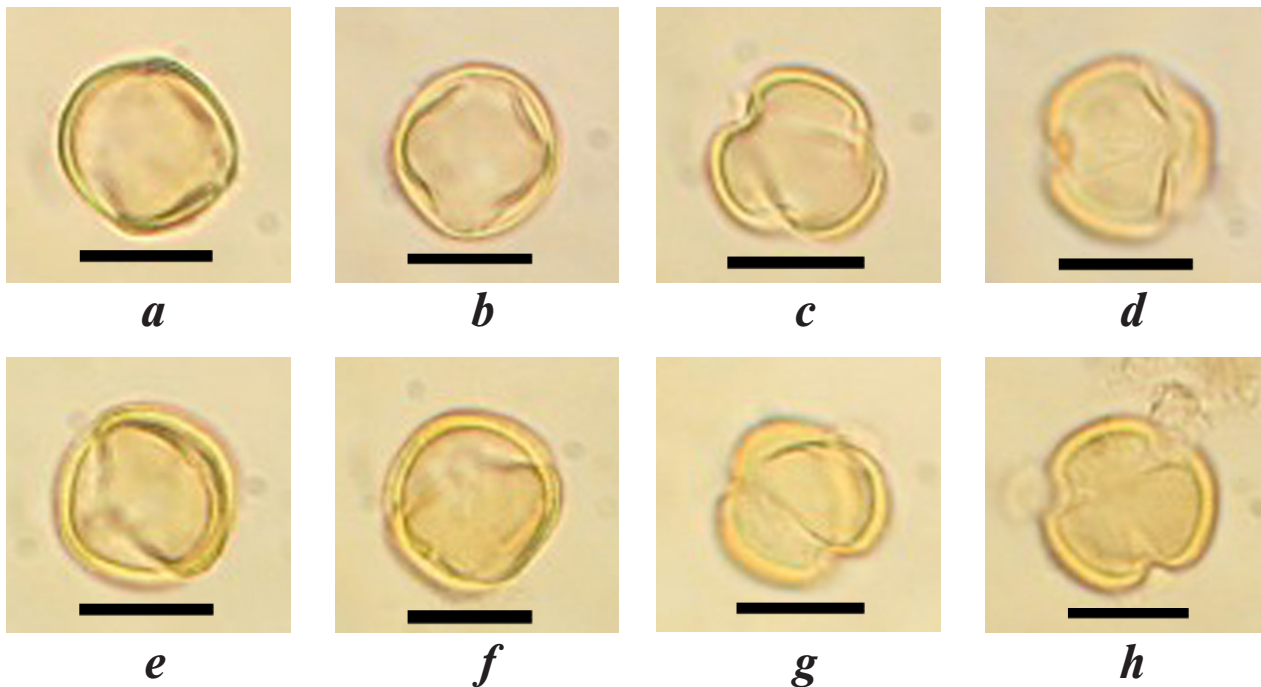


Fig. 4. Pollen grains of *Lindenbergia* (light microscopy): *a–d* – *L. philippensis*; *e–h* – *L. sinaica*; *a, b, e, f* – equatorial view; *c, d, g, h* – polar view. Scale bars: 10 μ m

Specimens investigated: 1. Ukrainian SSR [now Ukraine], Kherson Region, Kakhovka District, between Lvovo [L'vove] and Kozatskoye [Kozats'ke] villages, slopes of a large ravine of western exposition, petrophilic steppe area, on limestone. 24 April 1972. V.V. Zaverukha, No. 058169 (KW) [Label in Russian: УССР, Херсонская обл., Каховский р-н, между селами Львово – Козацкое, склоны большой балки западной экспозиции, степной участок петрофильного х-ра, на известняках. 24.IV 1972. Б.В. Заверуха. № 058169]. 2. [Ukraine] Mykolayiv Region, Snigurivka town, limestone slopes at the Ingulets River. 20 April 1972. L. Krytzka, No. 040211 (KW) [Label in Ukrainian: Миколаївська обл., м. Снігурівка, вапнякові схили на р. Інгулець. 20.IV 1972. Л. Крицька. № 040211].

Genus *Siphonostegia* Benth.

Siphonostegia chinensis Benth. (Fig. 3, *d–f*; Fig. 5, *m–p*)

LM. Pollen grains 3-colpate, oblate-spheroidal, spheroidal, occasionally prolate, in polar view circular, in equatorial view circular. P = 22.6–29.3 μ m, E = 25.3–29.3 μ m. Colpi long, narrow, 1.3–2.4 μ m wide, with indistinct, uneven margins, tapering to blunt ends, colpus membrane granulate. Mesocolpium = 18.6–

22.6 μ m, apocolpium = 5.3–9.3 μ m. Exine 1.3–2.4 μ m thick. Tectum nearly equal to infratectum. Columellae distinct, thin, arranged more or less regularly. Exine sculpture distinct, microreticulate.

SEM. Sculpture retipilate. Caput of pila 0.16–0.25 μ m. Colpus membrane granulate.

Specimen investigated: [Russia, Russian Far East] Primorye Province, near Khabarovsk city, in sands. 11 July 1910. N. Desoulavi (KW) [Label in Latin and Russian: Herbarium Florae Rossicae. Prov. Primorskaja, pr. urb. Chabarowsk, in arenosis. 11.VII 1910. Н. Десулави].

Original and published data on quantitative and qualitative pollen characters of representative of *Cymbarieae* and *Lindenbergieae* are summarized in Tables 1 and 2.

Comparative pollen morphology of genera of *Cymbarieae* and *Lindenbergieae*

In general, our data are in good agreement with the results of previous studies (Inceoğlu, 1982; Minkin, Eshbaugh, 1989; Lu et al., 2007). Analysis of our original palynomorphological data and literature records demonstrated that pollen grains of representatives of all genera of *Cymbarieae* are characterized by the 3-colpate type of apertures, mainly with retipilate sculpture (Table 2).

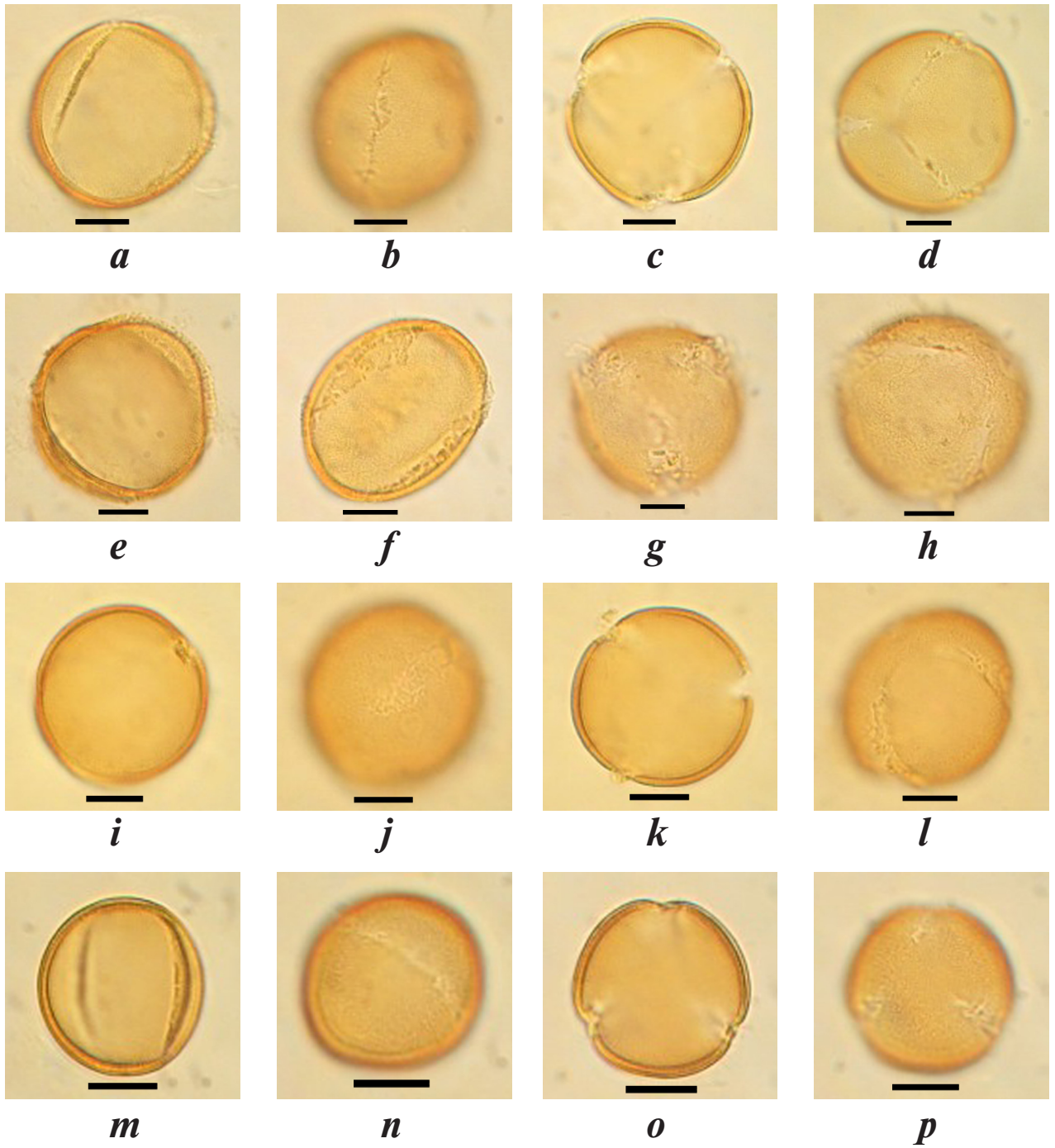


Fig. 5. Pollen grains of *Bungea*, *Cymbaria*, *Cymbochasma*, and *Siphonostegia* (light microscopy): *a–d* – *B. trifida*; *e–h* – *C. dahurica*; *i–l* – *C. borysthena*; *m–p* – *S. chinensis*. *a, b, e, f, i, j, m, n* – equatorial view; *c, d, g, h, k, l, o, p* – polar view. Scale bars: 10 μm .

Table 1. Summary of pollen morphometric features

Taxon	Polar axis (µm)	Equatorial axis (µm)	Colpi width (µm)	Mesocolpium (µm)	Apocolpium (µm)	Exine (µm)	Reference
<i>Lindenbergia philippensis</i>	13.3–17.3	14.6–18.6	1.3–2.7	9.3–10.6	2.7–4.0 (5.3)	1.1–1.6	original data
<i>Lindenbergia sinaica</i>	14.6–18.6	13.3–17.3	2.0–2.4	7.9–10.6	3.3–4.0	0.7–1.1	original data
<i>Bungea trifida</i>	38.6–47.9	34.6–43.9	2.4–3.3	26.6–34.6	6.6–13.3	1.3–3.3	original data
<i>Bungea trifida</i>	35	39	–	–	7	1.1	Inceoğlu, 1982
<i>Cymbaria dahurica</i>	37.2–47.9	33.2–42.6	4.0–6.6	26.6–33.2	10.6–19.9	1.6–2.7	original data
<i>Cymbaria dahurica</i>	32.5–42.5	27.5–35.0	–	–	–	–	Lu et al., 2007
<i>Cymbaria mongolica</i>	37.5–50.0	30.0–40.0	–	–	–	–	Lu et al., 2007
<i>Cymbochasma borysthénica</i>	29.3–33.2	30.6–35.9	2.7–5.3	22.6–26.6	6.6–9.3	0.7–1.3	original data
<i>Monochasma savatieri</i>	32.5–43.8	27.5–41.3	–	–	–	–	Lu et al., 2007
<i>Siphonostegia chinensis</i>	22.6–29.3	25.3–29.3	1.3–2.4	18.6–22.6	5.3–9.3	1.3–2.4	original data
<i>Siphonostegia chinensis</i>	22.1	22.4	–	–	–	–	Minkin, Eshbaugh, 1989
<i>Siphonostegia chinensis</i>	22.5–30.0	23.8–32.5	–	–	–	–	Lu et al., 2007
<i>Siphonostegia syriaca</i> (<i>Lesquereuxia syriaca</i>)	24	24	–	–	11	0.8	Inceoğlu, 1982
<i>Schwalbea americana</i>	27.2	27.2	–	–	–	–	Minkin, Eshbaugh, 1989

Original data are those reported here and in Table 2; "–" means no data reported.

Table 2. Summary of pollen morphological characteristics

Taxon	Apertures	Shape	Polar view	Colpi	Colpus membrane	Exine sculpture/ caput of pila	Reference
<i>Lindenbergia philippensis</i>	3-colporate	oblate-spheroidal, spheroidal (some prolate)	trilobate	long, narrow, acute ends	smooth	reticulate	original data
<i>Lindenbergia sinaica</i>	3-colporate	prolate, spheroidal (some oblate-spheroidal)	trilobate	long, narrow, acute ends	smooth	reticulate	original data
<i>Bungea trifida</i>	3-colpate	prolate (some spheroidal)	sub-triangular, circular	long, medium-width, acute ends	granulate	retipilate, 0.17–0.33	original data
<i>Bungea trifida</i>	3-colpate	oblate-spheroidal	semi-angular	long, acute ends	coarsely granulate	retipilate	Inceoğlu, 1982
<i>Cymbaria dahurica</i>	3-colpate	prolate (some oblate-spheroidal)	sub-triangular	medium-length, wide, blunt or acute ends	granulate	retipilate, rugulate-retipilate, 0.41–0.67	original data
<i>Cymbaria dahurica</i>	3-colpate	subprolate	sub-triangular	wide at equator and narrow near poles	with granules	retipilate, 0.45–0.90	Lu et al., 2007
<i>Cymbaria mongolica</i>	3-colpate	subprolate	sub-triangular	narrow, long and sunken	with granules	retipilate, 0.16–0.40	Lu et al., 2007
<i>Cymbochasma borysthénica</i>	3-colpate (some 4-colpate)	oblate-spheroidal	sub-circular	medium-length, medium-width, blunt, indistinct ends	granulate	retipilate, 0.17–0.25	original data
<i>Monochasma savatieri</i>	3-colpate	prolate, spheroidal (some oblate-spheroidal)	circular	wide at equator and narrow near poles	with fine granules	retipilate, 0.19–0.39	Lu et al., 2007
<i>Siphonostegia chinensis</i>	3-colpate	spheroidal, oblate-spheroidal (some prolate)	circular	long, narrow, blunt ends	granulate	retipilate, 0.16–0.25	original data
<i>Siphonostegia chinensis</i>	3-colpate	spheroidal	–	–	–	retipilate	Minkin, Eshbaugh, 1989
<i>Siphonostegia chinensis</i>	3-colpate	spheroidal	circular	wide at equator, but not narrow near poles	with coarse granules	retipilate, 0.18–0.31	Lu et al., 2007
<i>Siphonostegia syriaca</i> (<i>Lesquereuxia syriaca</i>)	3-colpate	prolate, spheroidal	circular	long, acute ends	coarsely granulate	retipilate	Inceoğlu, 1982
<i>Schwalbea americana</i>	3-colpate	spheroidal	–	–	–	retipilate	Minkin, Eshbaugh, 1989

Pollen grains in *Cymbochasma borysthenica* are 3-colpate and occasionally 4-colpate (Tsymbalyuk, 2011). They have the thinnest exine (0.7–1.3 μm) among pollen grains of the studied species of the tribe. Pollen grains of *Cymbochasma borysthenica* are smaller as compared to pollen of *Cymbaria dahurica* and *C. mongolica*, and also differ from species of *Cymbaria* sensu stricto in the pollen shape and outline (see Table 2). Thus, pollen characters may provide additional evidence in favor of recognition of *Cymbochasma* as a separate genus.

The two studied species of *Cymbaria* sensu stricto are similar in their pollen size, shape, and outline; however, they differ in their colpi structure and exine sculpture. In pollen grains of *Cymbaria dahurica*, colpi are medium-length, wider than in *C. mongolica*, and exine sculpture is retipilate (caput of pila 0.41–0.90 μm) or rugulate-retipilate, while *C. mongolica* has narrower and longer colpi (as compared to those in *C. dahurica*) and retipilate exine sculpture (caput of pila 0.16–0.40 μm) (Lu et al., 2007, and original data).

In general, pollen grains of *Bungea trifida* and *Cymbaria mongolica* (Lu et al., 2007) are similar in their shape, outline, size, and exine sculpture; however, *Bungea trifida* has colpi wider than those in *C. mongolica*, and the thickest exine (1.3–3.3 μm) among all studied species.

The smallest sizes are characteristic of pollen grains of *Siphonostegia chinensis* (Table 1). This species also has the narrowest colpi among all studied species. Columellae in all species studied here are mainly indistinct, while in *Siphonostegia chinensis* those are distinct, thin, and arranged more or less regularly.

Pollen grains of *Siphonostegia syriaca* (*Lesquereuxia syriaca*) (Inceoğlu, 1982) and *S. chinensis* are similar in their shape, outline, size, exine sculpture, and length of colpi; however, in *S. syriaca* the colpi ends are acute, while in *S. chinensis* they are obtuse (with blunt ends).

Pollen grains of *Schwalbea* (Minkin, Eshbaugh, 1989) are similar to those of *Siphonostegia* in their outline, size, and exine sculpture. Unfortunately, the characters reported by Minkin and Eshbaugh (1989) are insufficient for a more detailed comparative analysis.

The two studied species of *Lindenbergia* are similar to each other in having the 3-colporate aperture type, reticulate exine sculpture, and long and narrow colpi. They, however, differ by the exine thickness: in *L. philippensis* the exine is 1.1–1.6 μm thick, the tectum is nearly equal to the infratectum, and columellae are indistinct or distinct, while in *L. sinaica*

the exine is thinner (0.7–1.1 μm thick), and exine layers are invisible (indistinct).

Comparison of palynomorphological and molecular phylogenetic evidence

According to molecular phylogenetic studies (Bennett, Mathews, 2006; McNeal et al., 2013), the clade of *Cymbarieae* is subdivided into two subclades. The subclade that includes *Bungea*, *Cymbaria*, *Cymbochasma*, and *Monochasma* is characterized by larger pollen grains and wider colpi, as compared to the subclade of *Siphonostegia* (including *Lesquereuxia*) and *Schwalbea*.

The earliest-branching clade of *Lindenbergia* is sister to the clade containing all other members of *Orobanchaceae*. Small-sized 3-colporate pollen grains with reticulate exine revealed in all studied taxa of *Lindenbergia* are similar to pollen of some representatives of *Plantaginaceae*, in particular, those of *Gratiroleae* (Tsymbalyuk, Mosyakin, 2013a, 2014; Tsymbalyuk, 2016). In our opinion, that superficial similarity does not reflect direct phylogenetic relationships of these taxa, but rather some recurrent patterns (plesiomorphic characters) appearing in several clades of *Lamiales*.

The genus *Paulownia* Siebold & Zucc. is currently placed phylogenetically as a group sister to *Orobanchaceae* (Olmstead et al., 2001; Oxelman et al., 2005; Bennet, Mathews, 2006; Schäferhoff et al., 2010; McNeal et al., 2013). Pollen grains of *Paulownia* are 3-colporate, with reticulate exine (Erdtman, 1952; Chen, 1983; Tsymbalyuk, 2014). In these characters, *Paulownia* is rather similar to *Lindenbergia*. However, *Paulownia* differ from *Lindenbergia* in having small- and medium-sized pollen grains (small in *Lindenbergia*), trilobate and sub-triangular in outline (only trilobate in *Lindenbergia*), with distinct orae (indistinct in *Lindenbergia*) and the colpus membrane smooth and granulate (only smooth in *Lindenbergia*). Some similarity with pollen of *Paulownia* and *Lindenbergia* is also observed in pollen grains of the phylogenetically still problematic genus *Wightia* Wall. (Zhou et al. 2014), which also has 3-colporate pollen with reticulate exine sculpture (Wei, 1989; Tsymbalyuk, 2014, 2016). However, in *Paulownia* and *Lindenbergia* orae are circular and colpi are tapered to acute ends, while *Wightia* has elliptical orae and colpi expanded to rounded ends.

Thus, the earliest-branching clade of *Orobanchaceae* (*Lindenbergieae*) is palynomorphologically similar to the clade sister to all *Orobanchaceae* (*Paulowniaceae*)

and to the currently phylogenetically unplaced (?) genus *Wightia*. These palynomorphological findings confirm the phylogenetic patterns currently revealed in basal *Orobanchaceae* and their closest relatives.

Main trends of pollen evolution in early-branching *Orobanchaceae*

We may conclude that the colpporate (most probably 3-colpporate) type of pollen grains could be ancestral in *Orobanchaceae*. This type is peculiar to members of Clade I (*sensu* McNeal et al., 2013) that includes *Lindenbergia* (3-colpporate pollen with reticulate exine sculpture and indistinct orae). Then, the colpate type probably evolved by reduction of orae; this type, with retipilate exine sculpture, is characteristic of representatives of Clade II, including *Siphonostegia*, *Schwalbea*, *Monochasma*, *Cymbaria*, *Cymbochasma*, and *Bungea*. A sculpture type transitional between reticulate and retipilate exine could be the rugulate-retipilate type observed in *Cymbaria dahurica*. In the large and diverse Clade III, which includes holoparasitic members of *Boschniakia* C.A. Mey. ex Bong., *Xylanche* Beck, *Kopsiopsis* (Beck) Beck, *Epifagus* Nutt., *Conopholis* Wallr., *Mannagettaea* Harry Sm., *Cistanche* Hoffmanns. & Link, *Diphelypaea* Nicolson, *Orobanche* L., *Phelipanche* Pomel, and the recently resurrected genus *Aphyllon* Mitch. (Schneider, 2016; Schneider, Moore, 2017), a greater diversity of aperture and exine sculpture types and patterns is observed (Tsymbalyuk, Mosyakin, 2013b, c; Zare et al., 2014; Piwowarczyk et al., 2015; Tsymbalyuk, 2016).

Thus, available palynomorphological data are well consistent with the phylogenetic patterns in early-branching *Orobanchaceae* (*Lindenbergieae* and *Cymbarieae*) and their relatives, which are currently revealed by molecular phylogenetic evidence (Bennett, Mathews, 2006; McNeal et al., 2013). The considerable pollen diversity in crown clades and subclades of *Orobanchaceae* evolved on the base of a few pollen types and subtypes, which were peculiar to hypothetical ancestors of *Orobanchaceae* and are probably preserved until now in the extant taxa of *Paulowniaceae* and *Orobanchaceae* trib. *Lindenbergieae*.

Data on pollen morphology also confirm the updated phylogeny-based taxonomic circumscription of *Cymbarieae* as outlined by Fischer (2004) and Olmstead (2016).

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Цимбалюк З.М., Мосякін С.Л. Палиноморфологічні особливості представників триб *Lindenbergiae* і *Symbarieae* та еволюція пилку в базальних кладах *Orobanchaceae*.

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З використанням світлової та сканувальної електронної мікроскопії досліджено морфологію пилкових зерен чотирьох видів з чотирьох родів триби *Symbarieae* та двох видів роду *Lindenbergia* триби *Lindenbergiae* (*Orobanchaceae*). Встановлено, що пилкові зерна триби *Lindenbergiae* 3-борозно-орові (зрідка 2-борозно-орові), еліпсоїдальні, сфероїдальні або сплющено-сфероїдальні за формою, дрібних розмірів, з сітчастою скульптурою екзینی. Пилкові зерна триби *Symbarieae* 3-борозні, зрідка 4-борозні, еліпсоїдальні, сфероїдальні або сплющено-сфероїдальні за формою, середніх або великих розмірів, з сітчасто-паличковою або зморшкувато-сітчасто-паличковою скульптурою екзینی. Особливості пилкових зерен представників триб *Symbarieae* і *Lindenbergiae* порівнюються з такими в *Paulowniaceae* і верхівкових кладах *Orobanchaceae*. Базальна клада *Orobanchaceae* (*Lindenbergiae*) за палиноморфологічними особливостями подібна до *Paulowniaceae* (сестринська клада до всіх *Orobanchaceae*) і *Wightia*. Палиноморфологічні висновки підтверджують філогенетичні закономірності, які виявлені у базальних *Orobanchaceae* та їхніх найближчих родичів. Зроблено висновок, що борозно-оровий (ймові-

рно, 3-борозно-оровий) тип пилкових зерен може бути предковим у родині *Orobanchaceae*. Різноманітність пилкових зерен у верхівкових кладах *Orobanchaceae* еволюціонувала на основі декількох типів і підтипів пилку, властивих гіпотетичним предкам *Orobanchaceae*; такі типи, ймовірно, збереглися в сучасних представників *Paulowniaceae* та *Lindenbergiae*.

Ключові слова: *Symbarieae*, *Lindenbergiae*, *Orobanchaceae*, еволюція пилку, морфологія пилку, систематика, філогенія

Цымбалюк З.Н., Мосякин С.Л. Палиноморфологические особенности представителей триб *Lindenbergiae* и *Symbarieae* и эволюция пыльцы в базальных кладах *Orobanchaceae*. Укр. бот. журн., 2018, 75(2): 123–136.

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С помощью световой и сканирующей электронной микроскопии изучены пыльцевые зерна четырех видов из четырех родов трибы *Symbarieae* и двух видов рода *Lindenbergia* трибы *Lindenbergiae* (*Orobanchaceae*). Установлено, что пыльцевые зерна трибы *Lindenbergiae* 3-бороздно-оровые (изредка 2-бороздно-оровые), эллипсоидальные, сфероидальные или сплющено-сфероидальные по форме, мелких размеров, с сетчатой скульптурой экзины. Пыльцевые зерна трибы *Symbarieae* 3-бороздные, изредка 4-бороздные, эллипсоидальные, сфероидальные или сплющено-сфероидальные по форме, средних или больших размеров, с сетчато-палочковой или морщинисто-сетчато-палочковой скульптурой экзины. Особенности пыльцевых зерен представителей триб *Symbarieae* и *Lindenbergiae* сравниваются с таковыми у *Paulowniaceae* и терминальных клад *Orobanchaceae*. Базальная клада в семействе *Orobanchaceae* (*Lindenbergiae*) по палиноморфологическим особенностям сходна с *Paulowniaceae* (сестринская клада по отношению к *Orobanchaceae*) и *Wightia*. Палиноморфологические данные подтверждают филогенетические закономерности, выявленные в настоящее время у базальных *Orobanchaceae* и их ближайших родственников. Сделан вывод о том, что бороздно-оровый (возможно, 3-бороздно-оровый) тип пыльцевых зерен может быть предковым в семействе *Orobanchaceae*. Разнообразие пыльцы *Orobanchaceae* развилось на основе нескольких типов и подтипов, которые были свойственны гипотетическим предкам *Orobanchaceae* и, вероятно, сохранились у современных представителей *Paulowniaceae* и *Lindenbergiae*.

Ключевые слова: *Symbarieae*, *Lindenbergiae*, *Orobanchaceae*, эволюция пыльцы, морфология пыльцы, систематика, филогенія