Pollen morphology of alpine butterworts (*Pinguicula* L., Lentibulariaceae)

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**Abstract**

The pollen morphology of *Pinguicula alpina*, *P. arventii*, *P. grandiflora* subsp. *grandiflora*, *P. grandiflora* subsp. *rosea*, *P. hirtiflora*, *P. leptoceras* *Rchb.*, *P. reichenbachiana* Schindler (endemic of Maritime Alps) and *P. vulgaris* L. (

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1. Introduction

*Pinguicula* L., the second largest genus of the family Lentibulariaceae, contains about 100 currently accepted species. They are distributed in arctic, temperate, Mediterranean and tropical areas of Eurasia, North America (Mexico has the largest number of species — 44; *Zamudio*, 2005), Central America, South America and Africa only in the northeasterly region of Morocco (*Zamudio et al.*, 1996; *Steiger*, 1998; *Degtyareva et al.*, 2004, 2006; *Cieslak et al.*, 2005). In Europe, 12 species were reported by *Casper* (1972), but this number was expected to change due to the description of new species; the most recent were described in Italy (*Tammaro and Pace*, 1987; *Casper and Steiger*, 2001; *Conti and Peruzzi*, 2006; *Anzaldi and Casper*, 2009) and in Spain (*Blanca et al.*, 1999). Alpine species are *P. alpina* L., *P. arventii Genty* (endemic of Cozie Alps), *P. grandiflora* Lam. subsp. *grandiflora*, *P. grandiflora* subsp. *rosea* (*Mueller*) *Casper* (endemic in the calcareous mountains near Grenoble, France), *P. leptoceras* *Rchb.*, *P. reichenbachiana* *Schindler* (endemic of Maritime Alps) and *P. vulgaris* L. (*Casper*, 1966; *Pignatti*, 1982; *Aeschimann et al.*, 2004; *Pascal et al.*, 2008; *Compostella et al.*, 2010). *P. hirtiflora* Ten. is reported by *Aeschimann et al.* (2004) and only one population is known in Roya Valley, France: this population is considered to have been introduced by man because it is out of the typical area of the species (Central-Eastern Mediterranean according to *Casper*, 1966) (*Peruzzi et al.*, 2004; *Steiger and Tassara*, 2006). Recently *Casper and Steiger* (2001) described *P. polandinii* *Steiger* et *Casper*, a new endemic species in the hilly region of North-Eastern Venetian Prealps, Italy.

Alpine *Pinguicula* are herbaceous perennial insectivorous plants having leaves in a basal rosette, zygomorphic flowers and capsular fruits. They grow in nutrient-poor and partially sunny wet habitats: mainly vertical dripping limestone cliffs (*Cratoneuron* plant communities often involved in the processes of the travertine formation), hydromorphic alpine meadows but also banks of oligotrophic marshes and acidic *Sphagnum* bogs. The geographical distribution, for all the species of the genus, is highly fragmented due to the peculiarity and rarity of these habitats.

The published data on the pollen morphology of butterworts are still few, old, incomplete and based mainly on light microscopy observations. We focused on previous papers about the same species even if studied in different areas of the world. Concerning the alpine species, the pollen grains of *P. vulgaris* (but also *P. alpina* and *P. villosa*) are polycorate (number of colpi 6–8), prolate spheroidal (39 × 37 μm), the exine is 2 μm thick and the sexine is finely reticulate (*Erdtman et al.*, 1961). *P. vulgaris* was studied also by *Sohma* (1975) and *Moore et al.* (1991). Morphological data about *P. grandiflora* pollen grains were provided for the first time by *Heslop-Harrison* (2004) which reported a similarity with the ones of *P. vulgaris*. Recently *Tsymbalyuk et al.* (2008) described, using LM and SEM, the pollen grains of Ukrainian populations of *P. vulgaris* and *P. alpina*. *P. alpina* is also reported by *Hesse et al.* (2009). Albanian populations of *P. hirtiflora* (var. *hirtiflora* and var. *louisii*) have been studied by *Shukla et al.* (2007) where a slight difference between the pollen grains of the two varieties was noticed.

Fossil pollen of *Pinguicula* has been recorded only by *Mitchell* (1954).
Aim of this study is: a) to increase the knowledge about the pollen morphology of butterworts belonging to the Alpine Region, b) to compare our palynological data with those of previous authors, c) to give a pollen key based on micromorphological and quantitative data resulting from the study of different populations of alpine butterworts, d) to provide a valuable tool for pollen diagrams.

2. Materials and methods

Pollen grains of 9 taxa of the genus Pinguicula (belonging to the flora of the Alps) were studied. Specimens of different populations were collected in the field (Table 1: Fig. 1) during springs 2003–2008 and identified according to Casper (1966, 1974), Pignatti (1982), Casper and Steiger (2001), Aeschimann et al. (2004) and Pascali et al. (2008). Only flowers at the anthesis were picked up for a total of ~10 flowers for each population.

The excisseeata are housed in the herbarium of the Department of Biology, University of Milano: Herbarium Universitatis Mediolanensis (MI).

The palynological terminology used is according to Punt et al. (2007) and Hesse et al. (2009).

2.1. Light microscopy (LM)

Only flowers with mature anthers were used. Some pollen grains, removed from the anthers, were hydrated with distilled water on filter paper as in Rodondi et al. (2004), fixed in 2.5% glutaraldehyde, and stained with 4,6-diamidino-2-phenylindole (DAPI) dissolved in McIlvain buffer to detect DNA (Vergne et al., 1987). The observations and stained with 4,6-diamidino-2-phenylindole (DAPI) dissolved in filter paper as in Rodondi et al. (2004), were obtained from the data of the density gradient of sucrose pads (Chissoe and Skvarla, 1974). The observation of P (polar axis) and E (equatorial diameter) of the density gradient of sucrose pads (Chissoe and Skvarla, 1974) or stained in a sequence of osmium (O) and thiocarbohydrazide (T) solutions known as OTOTO method (Chissoe et al., 1995), was observed using a Leica 1430 and a Cambridge Stereoscan 360 scanning electron microscopes.

3. Results

3.1. LM survey (Plate I; Table 2)

The mature pollen grains of the investigated species of Pinguicula are released as free monads of medium size (~30 μm) (Plate I, 1–8). The pollen colour varies from whitish to yellow. Each grain is trinucleate (3-celled) (Plate I, 1).

Moreover, the grains are isopolar, stephanocporate, zonocolporate. Each aperture is associated with a colpus that is perpendicular to the equator and a bridge or constriction which seems to divide the colpus into two parts is often visible (Plate I, 3, 7). The number of colpori varies from species to species with a minimum of (4)–(5)–(6) colpori in P. grandiflora subsp. rosea, and a maximum of ~8 (10) colpori in P. hirtiflora. Moreover the two subspecies of P. grandiflora show a different shape and number of colpori: suboblate and (5)–(6)–(7)–(8) colpori in subsp. grandiflora (Plate I, 2); oblate spheroidal and (4)–(5)–(6) colpori in subsp. rosea (Plate I, 3). Pollen grains of P. poldinii show a large number of anastomosing colpori. Around 60%, of the approximately 800 grains observed, has this characteristic feature, which makes these grains asymmetric and anomalous (Plate I, 7). The pollen grains of Pinguicula in polar view have a circular equatorial outline and the shape is oblate spheroidal. In P. reichenbachiana prolate pollen grains are the most frequent (Plate I, 8).

3.2. SEM survey (Plates II–V; Table 2)

Each grain is stephanocporate and its pores have a rectangular profile (Plate IV, 5; Plate V, 5, 9). The colpus membrane is often covered with granular elements (Plate III; 4) and the colpi are not normally fused at the polar edge. The inner structure of the sporoderm of some broken pollen grains was observed: there are two patterns of exine, one with a nearly continuous tectum like in P. hirtiflora, the other with a discontinuous tectum like in P. reichenbachiana (Plate II, 1–2).

### Table 1

<table>
<thead>
<tr>
<th>Species</th>
<th>Site (see also Fig. 1)</th>
<th>Elevation (m a.s.l.)</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. alpina L.</td>
<td>1a – Alpe Gera (SO, Italy)</td>
<td>2100</td>
<td>Neutrophile alpine grasslands</td>
</tr>
<tr>
<td></td>
<td>1b – Monte Alben (BG, Italy)</td>
<td>1500</td>
<td>Carex firma, hydromorphic alpine grasslands, NE slope</td>
</tr>
<tr>
<td></td>
<td>1c – Grigna Settecentronale (LC, Italy)</td>
<td>1600</td>
<td>Carex firma, hydromorphic alpine grasslands, SE slope</td>
</tr>
<tr>
<td></td>
<td>2 – Pian del Re, Monviso, Cisallo (CN, Italy)</td>
<td>2020</td>
<td>Acidophilous bog</td>
</tr>
<tr>
<td>P. arvetii Gentry</td>
<td>3 – Rutor Valley (AO, Italy)</td>
<td>2135</td>
<td>Alpine heath</td>
</tr>
<tr>
<td>P. grandi/flora Lam. subsp. grandiflora*</td>
<td>4 – Chaparellan (Département Isère, France)</td>
<td>1000</td>
<td>Wet banks of a sandy stream</td>
</tr>
<tr>
<td></td>
<td>5 – Fontan, Val Roya (Département Alpes-Maritimes, France)</td>
<td>520</td>
<td>Dripping limestone cliffs</td>
</tr>
<tr>
<td>P. leptoceras Rchb.</td>
<td>6a – Monte Alben (BG, Italy)</td>
<td>1500</td>
<td>Carex firma, hydromorphic alpine grasslands, SE slope</td>
</tr>
<tr>
<td></td>
<td>6b – Alpe Lago, Chiesa Val Malenco (SO, Italy)</td>
<td>1620</td>
<td>Marshes</td>
</tr>
<tr>
<td></td>
<td>6c – Val Porcellizzo, Val Masino (SO, Italy)</td>
<td>1800</td>
<td>Wet acidophilous grasslands</td>
</tr>
<tr>
<td></td>
<td>6d – Pian dell’acqua nera, Passo S. Marco (BG, Italy)</td>
<td>1750</td>
<td>Acidophilous bog</td>
</tr>
<tr>
<td>P. poldinii Steiger et Casper</td>
<td>7 – Campone, Tramonti di Sotto (PN, Italy)</td>
<td>450</td>
<td>Dripping limestone cliffs</td>
</tr>
<tr>
<td>P. reichenbachiana Schindler*</td>
<td>8a – Fontan, Val Roya (Département Alpes-Maritimes, France)</td>
<td>520</td>
<td>Dripping limestone cliffs</td>
</tr>
<tr>
<td></td>
<td>8b – Villaggio Rocca Barbera (SV, Italy)</td>
<td>800</td>
<td>Dripping limestone cliffs</td>
</tr>
<tr>
<td></td>
<td>9a – Saune D’Oulx (TO, Italy)</td>
<td>1500</td>
<td>Wet meadows</td>
</tr>
<tr>
<td></td>
<td>9b – Passo Campo Carlo Magno, Pinzolo (TN, Italy)</td>
<td>1620</td>
<td>Wet meadows</td>
</tr>
<tr>
<td></td>
<td>9c – Col di Tende (Département Alpes-Maritimes, France)</td>
<td>1250</td>
<td>Dripping limestone cliffs</td>
</tr>
<tr>
<td></td>
<td>9d – Chaparellan (Département Isère, France)</td>
<td>1000</td>
<td>Wet meadows</td>
</tr>
</tbody>
</table>

* As P. grandi/flora Lam. subsp. grandi/flora

* As P. longifolia Ram. var. reichenbachiana (Schindler) Roxy or P. longifolia subsp. reichenbachiana (Schindler) Casper.
The exine ornamentation of *P. hirtiflora* is perforate (Plate IV, 4), while the ornamentation of all the other investigated species is rugulate–microreticulate or rugulate–reticulate (*P. alpina*) (Plate III, 2, 4, 6; Plate IV, 2, 6; Plate V, 3, 6, 9).

3.2.1. *P. alpina* (Plate III, 1–2)

The grains are suboblate, radially symmetric, isopolar and zonocolporate with (5)–6–7 (6) colpori. Rare anastomoses of colpori apices are visible. The profile of colpus margin is irregular and there are granules on the colpus membrane. The sexine ornamentation is rugulate–reticulate with thick curved muri (~1.0 μm thick), irregular narrow lumina (often wider than 1.0 μm) and rare perforations on the mesocolpium margin. There is usually no differentiation of the sexine towards the poles and/or colpori.

3.2.2. *P. arvetii* (Plate III, 3–4)

The grains are oblate spheroidal, radially symmetric, isopolar and zonocolporate with 5–6–7 (8) colpori. Anastomoses of colpori between the polar margins are very rare. The sexine ornamentation is rugulate–microreticulate, near the margin of the colpi, the muri merge and lumina become smaller, resembling perforations. Lumina are very variable in size and shape (rounded or polygonal) and they are rarely wider than 1.0 μm. The muri are thick (thickness 0.5–1.0 μm).

3.2.3. *P. grandiflora* (Plate III, 5–6; Plate IV, 1–2)

In *P. grandiflora* the grains are suboblate in subsp. *grandiflora* and oblate spheroidal in subsp. *rosea.* The grains are radially symmetric, isopolar and zonocolporate with (5)–6–7–8 (8) colpori in subsp. *grandiflora*; (4)–5–6 (6) colpori in subsp. *rosea.* Rare anastomoses of colpori apices are visible. The sexine ornamentation is rugulate–microreticulate with thin curved muri (0.2–0.5 μm thick) and the lumina are very variable in size and shape (rarely wider than 1.0 μm). There is usually no differentiation of the sexine towards the poles and/or colpori.

3.2.4. *P. hirtiflora* (Plate II, 1; Plate IV, 3–4)

The grains are oblate spheroidal, radially symmetric, isopolar, zonocolporate and parasyncolporate with 8–9–10 (10) colpori. The tectum is nearly continuous and perforated. Puncta (diameter <0.5 μm) have different shapes and sizes and their density on the mesocolpium margins and on the apocolpium is lower. The splitting of some pollen grains allowed observation of the thickness of the sporoderm layers: foot layer (0.2 μm), columnellae (0.4 μm), tectum (0.4 μm). The whole thickness is around 1.0 μm.

### Table 2

Biometric measures, based on 50 pollen grains for each population, of the examined taxa. Abbreviations: P = polar axis; E = equatorial diameter; SO = suboblate; OS = oblate spheroidal; PS = prolate spheroidal; S = spheroidal.

<table>
<thead>
<tr>
<th>Species</th>
<th>P (μm)</th>
<th>E (μm)</th>
<th>P/E</th>
<th>Shape</th>
<th>Sexin ornamentation</th>
<th>Muri width (μm)</th>
<th>Number of colpori</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. alpina</em></td>
<td>27.5 ± 0.15</td>
<td>32.1 ± 0.15</td>
<td>0.86</td>
<td>SO</td>
<td>Rugulate–reticulate</td>
<td>~1.0</td>
<td>(5)–6–7–(8)</td>
</tr>
<tr>
<td><em>P. arvetii</em></td>
<td>28.5 ± 0.29</td>
<td>29.9 ± 0.28</td>
<td>0.96</td>
<td>OS</td>
<td>Rugulate–microreticulate</td>
<td>0.5–1.0</td>
<td>5–6–7</td>
</tr>
<tr>
<td><em>P. grandiflora</em></td>
<td>26.3 ± 0.28</td>
<td>32.1 ± 0.29</td>
<td>0.84</td>
<td>SO</td>
<td>Rugulate–microreticulate</td>
<td>0.2–0.5</td>
<td>(5)–6–7–(8)</td>
</tr>
<tr>
<td><em>P. rosea</em></td>
<td>28.6 ± 0.31</td>
<td>31.2 ± 0.29</td>
<td>0.92</td>
<td>OS</td>
<td>Rugulate–microreticulate</td>
<td>0.2–0.5</td>
<td>(4)–5–6</td>
</tr>
<tr>
<td><em>P. hirtiflora</em></td>
<td>29.4 ± 0.25</td>
<td>33.3 ± 0.26</td>
<td>0.88</td>
<td>OS</td>
<td>Perforate</td>
<td>~</td>
<td>8–9–10</td>
</tr>
<tr>
<td><em>P. leptoceras</em></td>
<td>28.9 ± 0.28</td>
<td>31.1 ± 0.26</td>
<td>0.93</td>
<td>OS</td>
<td>Rugulate–microreticulate</td>
<td>0.5–1.0</td>
<td>5–6–7–(7)</td>
</tr>
<tr>
<td><em>P. poldini</em></td>
<td>31.3 ± 0.20</td>
<td>34.7 ± 0.27</td>
<td>0.90</td>
<td>OS</td>
<td>Rugulate–microreticulate</td>
<td>0.5–1.0</td>
<td>6–7</td>
</tr>
<tr>
<td><em>P. reichenbachiana</em></td>
<td>30.2 ± 0.26</td>
<td>29.1 ± 0.23</td>
<td>1.04</td>
<td>PS</td>
<td>Rugulate–microreticulate</td>
<td>0.2–0.5</td>
<td>5–6</td>
</tr>
<tr>
<td><em>P. vulgaris</em></td>
<td>32.3 ± 0.14</td>
<td>32.4 ± 0.13</td>
<td>1.00</td>
<td>S</td>
<td>Rugulate–microreticulate</td>
<td>0.5–1.0</td>
<td>6–7–(8)</td>
</tr>
</tbody>
</table>

Fig. 1. Map of sites of the investigated species (see also Table 1): 1 (a, b, c) = *P. alpina*; 2 = *P. arvetii*; 3 = *P. grandiflora* subsp. *grandiflora*; 4 = *P. grandiflora* subsp. *rosea*; 5 = *P. hirtiflora*; 6 (a, b, c, d) = *P. leptoceras*; 7 = *P. poldini*; 8 (a, b) = *P. reichenbachiana*; 9 (a, b, c, d) = *P. vulgaris.*
3.2.5. *P. leptoceras* (Plate IV, 5–6)

The grains are oblate spheroidal, radially symmetric, isopolar and zonocolporate with 5–6–(7) colpori. Anastomoses of colpori between the polar margins are very rare. The sexine ornamentation is rugulate-microreticulate, near the margin of the colpi, the muri merge and lumina become smaller, resembling perforations. Lumina
are very variable in size and shape (rounded or polygonal) and they are rarely wider than 1.0 μm. The muri are thick (thickness 0.5–1.0 μm).

3.2.6. P. poldinii (Plate V, 1–3)

The grains are oblate spheroidal, radially symmetric or asymmetric, isopolar and zonocolporate with 6–7 colpori. Many different types of anastomosing colpori are often visible on the grain. The sexine ornamentation is rugulate–microreticulate, near the margin of the colpi, the muri merge and lumina become smaller, resembling perforations. Lumina are very variable in size and shape (rarely wider than 1.0 μm) while the muri are thick (thickness 0.5–1.0 μm).

3.2.7. P. reichenbachiana (Plate II, 2; Plate V, 4–6)

The grains are prolate spheroidal, radially symmetric, isopolar and zonocolporate with 5–6 colpori and rarest anastomoses close to the polar margins. The sexine ornamentation is rugulate–microreticulate, near the margin of the colpi, the muri merge and lumina become smaller resembling perforations. Lumina are variable in size and their shape is often circular (rarely wider than 1.0 μm). The muri are thin (thickness 0.2–0.5 μm). The splitting of some pollen grains allowed observation of the thickness of the sporo dermal layers: foot layer (0.4 μm), columellae (0.4 μm), tectum (0.5 μm). The whole thickness is around 1.3 μm.

3.2.8. P. vulgaris (Plate V, 7–9)

The grains are spheroidal, radially symmetric, isopolar and zonocolporate with 6–7–8 colpori. Anastomoses between the polar margins are very rare. The sexine ornamentation is rugulate–microreticulate, near the margin of the colpi, the muri merge and lumina become smaller, resembling perforations. Lumina are very variable in size and shape (rarely wider than 1.0 μm). The muri are thick (thickness 0.5–1.0 μm).

Table 2 summarizes the main features.

4. Discussion

The institution of Pinguicula poldinii as a new species (Casper and Steiger, 2001), the discovery of new sites for P. arvetii (Pascal et al., 2008) and P. grandiflora subsp. grandiflora (Compostella et al., 2010) as new species of the Italian flora, together with the fact that the palynological data are still few, old and based mainly on light microscopy investigations, induced a methodical research on the micromorphology of the pollen grains of butterworts belonging to Alpine flora.

The comparative LM and SEM analysis of the pollen grains of the nine investigated taxa confirmed the general typology of the pollen grains of Pinguicula L. Detailed palynomorphological characteristics of the not yet investigated species P. arvetii, P. grandiflora (two subspecies), P. leptoceras, P. poldinii, P. reichenbachiana are provided for the first time.

In all the species of Pinguicula the pollen grains are released as monads which are isopolar, radially symmetric, stephanoaperturate, zonocolporate and trinucleate (3-celled). The pollen colour, on fresh material, does not have any diagnostic relevance. The number of colpori is lower than 8, except in P. hirtiflora in which the number of colpori rises up to 10. The shape is from suboblate to oblate spheroidal (P< E), except for P. reichenbachiana, that is prolate spheroidal (P>E) (Table 2).

According to the pollen terminology (Punt et al., 2007; Hesse et al., 2009) the rugulate–microreticulate or rugulate–reticulate ornamentation characterizes the pollen wall of the butterworts investigated; only P. hirtiflora has a perforate ornamentation. P. alpina shows a rugulate–reticulate ornamentation characterized by very thick (around 1.0 μm) and twisted muri that make the lumina very narrow and irregular; the lumina sometimes are simple perforations. The microreticulum of P. arvetii, P. leptoceras, P. poldinii and P. vulgaris present thick muri (0.5–1.0 μm) in contrast with the thin muri (0.2–0.5 μm) of P. grandiflora (subsp. grandiflora and subsp. rosea) and P. reichenbachiana. The reticulum meshes of these last two species are larger than the one of the previous four species but nevertheless the ornamentation is still microreticulate. P. grandiflora and P. reichenbachiana differ because the first one has the muri more twisted and

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its sexine ornamentation usually do not differentiate towards the poles and/or colpori. The microreticulate ornamentation of the mesocolpium margin (around 2.0 μm) changes from reticulate to perforate and the tectum varies from discontinuous to nearly continuous in almost all the taxa but not in P. alpina and P. grandi flora (subsp. grandi flora and subsp. rosea).

The perforate sexine ornamentation of P. hirtiflora shows a drastic reduction of puncta density near the margin of mesocolpium and on apocolpium.

The pollen of P. poldinii is very peculiar: around 60%, of the nearly 600 pollen grains observed, showed a large number of anastomoses between colpori and the grains are often asymmetric and anomalous. The anastomoses are very irregular and involve each part of the grain. Often it is impossible to distinguish between the polar and the equatorial region (Table 2); a similar feature has been reported also in Utricularia brennii Heer (Lentibulariaceae) (Huynh, 1968; Casper and Manitz, 1975; Käsermann and Moser, 1999). Casper and Steiger (2001) described briefly the pollen grains of P. poldinii and they found 6–8-colporate grains; even if we have never found 8-colporate grains we use this value to complete the proposed pollen key (Table 3).

The exine micromorphology by itself does not allow a clear separation of P. arvetii, P. leptoceras, P. poldinii and P. vulgaris. There are small differences regarding: the shape, the size and the number of colpori. Grains of P. vulgaris are spheroidal while they are oblate spheroidal in the other three species. Pollen grains of P. vulgaris and P. poldinii are larger than the ones of P. arvetii and P. leptoceras. 5-colporate pollen grains are frequent in P. arvetii and P. leptoceras while they have never been observed in P. poldinii and P. vulgaris (their minimum is 6-colporate) (Table 2). P. arvetii is so close to P. leptoceras that it is difficult to separate them properly using palynological data. LM observations combined to draw up a pollen key (Table 3) for the identification of the different species. This pollen key is an important tool for pollen diagrams and consequently for the reconstruction of paleo-wet oligotrophic-environments through the Holocene.

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Plate III.

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Plate V (caption on p. 6).

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Table 3

Pollen key.

1. Tectum nearly continuous with a perforate ornamentation, number of colpori ≥ 8

1. Tectum discontinuous with a rugulate-microreticulate or rugulate-reticulate ornamentation, number of colpori ≤ 8

2. Tectal muri thin: 0.1–0.5 μm thick

2a. Prolate spheroidal shape, rugulate-microreticulate ornamentation, 5–6 colpori

3b. Subulate shape, rugulate-microreticulate ornamentation with twisted muri, (5)–6–7–(8) colpori

3c. Oblate spheroidal shape, rugulate–microreticulate ornamentation with twisted muri, (4)–5–(6) colpori

2. Tectal muri thick: 0.5–1.0 μm thick

4. Subulate shape, rugulate–reticulate ornamentation with compact and twisted muri (~1.0 μm thick)

4a. Shape from oblate spheroidal to spheroidal, rugulate–microreticulate ornamentation with muri 0.5–1.0 μm thick

5. Spheroidal shape, P and E = 30 μm, 6–7–(8) colpori

5a. P = E = 30 μm, 5–6–(7) colpori

6b. P = 30 μm and E = 30 μm, 5–6–(7) colpori

6c. P and E = 30 μm, 6–7–(8) colpori

As our data, (6–7) colpori, combined with Casper and Steiger (2001), 6–8 colpori.

References


