A preliminary account of the peristome structure and spores in six species of *Philonotis* (Bartramiaceae, Bryophyta)

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**Abstract** – A morphological study of the peristome and spores of six species of European *Philonotis* is reported. New peristome and spore characters are described and discussed. Among them the characters that show consistent differences and could help with accurate discrimination of the species are the papillosity of the surface of the endostome and exostome teeth, the differentiation of the OPL median line, the papillosity and number of cell rows of the basal membrane of the exostome and endostome, the number of cilia per cluster, and spore ornamentation. Nevertheless a more intensive study and examination of more numerous specimens is needed to confirm the taxonomic value of these characters.

*Philonotis* / Peristome / SEM / Exostome / Endostome / Outer Peristomial Layer / Principal Peristomial Layer / Inner Peristomial Layer / Intertrabecular thickenings / Ornamentation / Spores

**INTRODUCTION**

*Philonotis* is a worldwide genus that comprises 169 species (Crosby *et al.*, 1999), most of which are distributed in the southern hemisphere. In Europe this genus is represented by only 9 species, *Philonotis caespitosa* Jur., *Ph. calcaria* (Bruch & Schimp.) Schimp., *Ph. capillaris* Lindb. ex Hartm., *Ph. cernua* (Mitt.) Griffin & Buck, *Ph. fontana* (Hedw.) Brid., *Ph. marchica* (Hedw.) Brid., *Ph. rigida* Brid., *Ph. seriata* Mitt. and *Ph. tomentella* Molendo in Lorentz. Among them only 6 have been found in different European herbaria with sufficient sporophytes to allow a study of the morphology and structure of the peristome and spores.

There are very few previous works on the peristome structure of *Philonotis*, and only drawings and light micrographs have been published. Dismier (1907) provided a good description of the exostome teeth. He described the presence of intertrabecular thickenings that he named “intertrabecular tori” and did not consider them to be taxonomically important. Zales (1973) described the structure of the endostome as “cohering cilia”, and Shaw & Rohrer (1984) correctly evaluated the structure as consisting of segments that split along their median line almost to the basal membrane, each half diverging towards the cilia where they often meet the corresponding half of the next adjacent segment, thus framing the cilia.

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In the same way, very little specific work has been done to date on the spore ornamentation of *Philonotis*. Boros & Járai-Komlódi (1975) described the spore ornamentation in *Philonotis calcaria* and *Ph. fontana*. Subsequently, Hirohama (1977), Griffin (1981, 1982) and Griffin & Acuña (1983) described the spore ornamentation in the genera of Bartramiaceae.

In the course of a taxonomic study of the genus *Philonotis* for the Flora Briottitca Ibérica, both peristome structure and spore ornamentation appeared to vary between the studied species. To confirm this variation, a SEM study of the peristome structure and spore ornamentation was carried out. Since the number of studied specimens was limited in number, this study was not intended to test taxonomic hypotheses, but rather to describe the variation in the morphological characters of the sporophyte.

**MATERIAL AND METHODS**

This study is based on the examination of more than 86 specimens from the following European herbaria: BM (London), FCO (Oviedo), GDA (Granada), H (Helsinki), Herb. J. Martínez-Abaigar (Logroño), LEB (León), MA-Musci (Madrid), MACB (Madrid), MUB (Murcia), SANT-Bryo (Santiago de Compostela), VAB (Valencia) and VIT (Vitoria) (See Appendix I for a list of selected specimens). Mature capsules and spores from them were taken for this study.

General morphology was examined using an Olympus CH-2 light microscope. In each of these preparations up to 20 measurements were made on the dimensions of the spores and peristome.

Spore and peristome surfaces were studied using a Jeol JSM-6100 scanning electron microscope (SEM), using 10-25 kv acceleration. For the SEM study, the material was fixed in 3% glutaraldehyde with 0.1M cacodylate buffer at 4°C, then washed in cacodylate and saccharose buffer, and dehydrated in an increasing acetone series, critical point dried and coated with a gold layer of 20-30 nm.

The nomenclature used for the description of the peristome structure follows Edwards (1984): OPL (Outer Peristomial Layer); PPL (Principal Peristomial Layer); IPL (Inner Peristomial Layer).

**RESULTS**


Exostome teeth 200-250 µm long, apex truncate; OPL (Fig. 1, A) with the median line well developed, the basal surface reticulate-papillose, the papillae 0.75-0.88 µm high, the apical surface with scattered tall papillae, 1.18-1.89 µm high; exostomial PPL (Fig. 1, C) trabeculate, smooth at the base and with wide, short and simple papillae extending to the apex, 0.41-0.48 µm high, with intertrabecular thickenings in the upper half, 8.4-11.6 µm high; basal membrane smooth and formed by 3-4 cell rows, 70-80 µm high. Endostome segments 100-140 µm long;
endostomial PPL (Fig. 1, D) with simple and irregular papillae throughout, 0.81-1.30 µm high; IPL (Fig. 1, B) smooth at the base, papillose in the upper third, the papillae simple, sometimes bifurcate and disposed in rows (Fig. 1, E), 1.24-1.55 µm high; cilia in clusters of 2-3, 60-100 µm long; basal membrane smooth, formed by 4-6 cell rows, 80-90 µm high. Peristomial formula 4:2:8.

Spores (Fig. 1, F) subspherical to reniform, 20-28 µm in diameter, perine with pilate processes, 1.70-2.02 µm high, finely granulate on the surface, often clustered at the level of the capitae into small, irregularly arranged groups that leave visible furrows in the exine surface.


Exostome teeth 250-290 µm long, apex blunt; OPL (Fig. 2, A-C) with the median line well developed, the basal surface reticulate-papillose, with simple papillae extending to the apex, the papillae 1.86-1.95 µm high; exostomial PPL (Fig. 2, D) trabeculate, finely papillose at the base, the papillae 0.62-1.15 µm high, strongly papillose in the upper third, with simple papillae, 0.51-0.59 µm high, with intertrabecular thickenings in the upper half; basal membrane smooth, formed by 3-4 cell rows, 50-70 µm high. Endostome segments 150-200 µm long, sometimes with perforations or thin areas in the wall (Fig. 2, F); endostomial PPL (Fig. 2, E-F) smooth at the base, finely papillose in the upper third, with simple papillae, 0.60-0.79 µm high; IPL (Fig. 2, G) finely papillose at the base, with high and irregular papillae, sometimes bifurcate or branched in the upper third, 0.64-2.36 µm high; cilia with incurved apex, in clusters of 3-4, 50-60 µm long; basal membrane smooth, formed by 3-5 cell rows, 70-90 mm high. Peristomial formula 4:2:10.

Spores (Fig. 2, H) subspherical to reniform, 24-26 µm in diameter, perine composed of bacute to pilate processes, 1.51-1.64 µm high, rarely coalescent, irregularly sized.

**Philonotis fontana** (Hedw.) Brid., *Bryol. Univ.* 2: 18. 1827.

Exostome teeth 100-150 µm long, apex truncate; OPL (Fig. 3, A-B) with the median line well developed, though sometimes not so, the basal surface rugose, sometimes with scattered papillae in the upper third; exostomial PPL (Fig. 3, C) trabeculate, smooth at the base, with thick and simple papillae in the upper third, 0.49-0.79 µm high, with intertrabecular thickenings in the upper half, 8.5 µm high; basal membrane formed by 3-4 cell rows, 70-80 µm high. Endostome segments 140-150 µm long; endostomial PPL (Fig. 3, D) rugulose throughout, the papillae 0.83-1.71 µm high; IPL (Fig. 3, E) very papillose, with simple papillae throughout, 1.21-1.71 µm high; cilia in clusters of 2-3, 100-130 µm long; basal membrane finely papillose, formed by 4-5 cell rows, 80-90 µm high. Peristomial formula 4:2:10.

Spores (Fig. 3, F) ovate to reniform, 24-28 µm in diameter, with diverse perinate processes, from granulae and verrucae to pila or clavae, 1.28-2.68 µm high, smooth on the surface, eventually clustered into small groups.


Exostome teeth 220-330 µm long, apex blunt; OPL (Fig. 4, A-C) with the median line well developed, the basal surface reticulate-smooth, papillose in the upper third, the papillae 0.96-1.15 µm high; exostomial PPL (Fig. 4, D-E) trabeculate, smooth at the base, papillose in the upper third, with simple papillae, 0.69-1.16 µm high, with intertrabecular thickenings in the upper half, 11.3-14.3 µm
Peristome structure and spores in *Philonotis*

high; basal membrane formed by 3 cell rows, 50-60 µm high. Endostome segments 220-330 µm long; endostomial PPL (Fig. 4, F-G) smooth at the base, weakly papilllose in the upper third, with simple and scattered papillae, 0.42-0.56 µm high; IPL smooth at the base, with papillose ridges near the apex, the papillae 1.05-1.23 µm high; cilia in clusters of 3, 90-100 µm long; basal membrane smooth, formed by 3-5 cell rows, 80-90 µm high. Peristomial formula 4:2:6.

Spores (Fig. 4, H) from subspherical to reniform, 32-34 µm in diameter, perine with pilum-like processes with relatively prominent capitae, 1.75-2.05 µm high, densely granulate on the surface, and often coalescent at the apex.
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Fig. 4. *Philonotis rigida*. **A**: Apical OPL and IPL. **B**: Apical OPL and endostomial PPL. **C**: Basal OPL. **D**: Apical exostomial PPL. **E**: Basal exostomial PPL. **F**: Apical endostomial PPL. **G**: Basal endostomial PPL. **H**: Spore.

Exostome teeth 140-180 µm long, apex truncate; OPL (Fig. 5, A) with the median line sometimes absent, surface reticulate-smooth throughout; exostomial PPL (Fig. 5, B) trabeculate, smooth at the base, upper third finely papillose, with intertrabecular thickenings in the upper third, 16 µm high; basal membrane (Fig. 5, C) formed by 3-6 cell rows, 60-90 µm high. Endostome segments 120-150 µm long; endostomial PPL (Fig. 5, D) smooth at the base; IPL (Fig. 5, E-G) finely papillose in the upper third, the papillae 0.56-0.60 µm high, with thinned areas in the walls; cilia in clusters of 2-3, 70-110 µm long; basal membrane finely papillose or smooth, formed by 4-5 cell rows, 80-90 µm high. Peristomial formula 4:2:8.

Spores (Fig. 5, H) spherical to reniform, 26-30 µm in diameter, perine consisting of predominantly bacula-like processes, 1.09-1.44 µm high, isolated, less often clustered into small groups.

Philonotis tomentella Molendo in Lorentz, Moosstudien: 170. 1864.

Exostome teeth 200-240 µm long, apex truncate; OPL (Fig. 6, A-B) with the median line well developed, the basal surface smooth, the middle porose, and the upper third smooth, sometimes with scattered papillae; exostomial PPL (Fig. 6, C) trabeculate, smooth at the base, finely papillose in the upper third, the papillae 0.37-0.56 µm high; basal membrane formed by 3-4 cell rows, 40-60 µm high. Endostome segments 100-150 µm long; endostomial PPL (Fig. 6, D) smooth at the base, finely papillose near the apex, the papillae 0.42-0.53 µm high; IPL (Fig. 6, E-F) finely papillose throughout; cilia in pairs, 90-100 µm long; basal membrane smooth, formed by 7 cell rows, 40-60 µm high. Peristomial formula 4:2:6.

Spores (Fig. 6, G-H) reniform, 24-26 µm in diameter, perine largely composed of pilum-like processes, which become verrucae towards the proximal surface, 1.04-1.42 µm high, smooth, clearly tending to cluster in their capitae.

DISCUSSION

The peristome in Philonotis may be double, simple or absent (Philonotis cernua (Mitt.) Griffin & Buck). The peristomial formula, following Edwards (1979, 1984), varies from 4:2:6 (Philonotis rigida, Ph. tomentella), to 4:2:8 (Philonotis caespitosa, Ph. seriata) and 4:2:10 (Philonotis calcarea, Ph. fontana).

The exostome is formed by 16 brownish or reddish triangular teeth, with an obtuse (Philonotis calcarea, Ph. rigida) or truncate apex (Philonotis caespitosa, Ph. fontana, Ph. seriata, Ph. tomentella). The OPL is usually reticulate-papillose, sometimes smooth (Philonotis tomentella, Ph. fontana) or reticulate-smooth (Ph. fontana, Ph. seriata) at the base, papillose near the apex, with a median line that is usually distinct, but sometimes less clear (Philonotis fontana, Ph. seriata). The exostomial PPL is trabeculate, usually smooth, sometimes papillose (Philonotis calcarea) at the base and densely papillose with intertrabecular thickenings in the upper third. The basal membrane of the exostome is formed by 3-6 rows of oblate, hyaline or brownish, smooth or lightly papillose cells (Table 1).

The endostome is formed by 16 double segments, articulate, hyaline, and variously fused together throughout or free at the apex. They alternate with
Fig. 5. *Philonotis seriata*. **A**: Basal OPL. **B**: Basal exostomial PPL. **C**: Basal membrane of exostome. **D**: Basal endostomial PPL. **E**: IPL view. **F**: Apical IPL with thinned areas in the wall. **G**: Basal IPL. **H**: Detail of the spore ornamentation.
Fig. 6. *Philonotis tomentella*. **A:** Apical OPL. **B:** Basal OPL with pores. **C:** Basal exostomial PPL. **D:** Basal endostomial PPL. **E:** Detail of apical IPL. **F:** Apical IPL. **G:** Spore. **H:** Detail of the spore ornamentation.
Table 1. Exostome characters in *Philonotis*.

<table>
<thead>
<tr>
<th></th>
<th>Length (µm)</th>
<th>Upper third (OPL)</th>
<th>Base (OPL)</th>
<th>Median line</th>
<th>Upper third (PPL)</th>
<th>Base (PPL)</th>
<th>Basal membrane</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ph. caespitosa</em></td>
<td>200-250</td>
<td>With high scattered papillae</td>
<td>Reticulate-papilllose</td>
<td>Well developed</td>
<td>Papilllose with intertrabecular thickenings</td>
<td>Smooth</td>
<td>3-4 cell rows</td>
</tr>
<tr>
<td><em>Ph. calcarea</em></td>
<td>250-290</td>
<td>With simple papillae</td>
<td>Reticulate-papillose</td>
<td>Well developed</td>
<td>Strongly papilllose with intertrabecular thickenings</td>
<td>Finely papillose</td>
<td>3-4 cell rows</td>
</tr>
<tr>
<td><em>Ph. fontana</em></td>
<td>100-150</td>
<td>Sometimes with scattered papillae</td>
<td>Rugose</td>
<td>Well developed, though sometimes not so</td>
<td>Papilllose with intertrabecular thickenings</td>
<td>Smooth</td>
<td>3-4 cell rows</td>
</tr>
<tr>
<td><em>Ph. rigida</em></td>
<td>220-330</td>
<td>Papillose</td>
<td>Reticulate-smooth</td>
<td>Well developed</td>
<td>Papilllose with intertrabecular thickenings</td>
<td>Smooth</td>
<td>3 cell rows</td>
</tr>
<tr>
<td><em>Ph. seriata</em></td>
<td>140-180</td>
<td>Reticulate-smooth</td>
<td>Reticulate-smooth</td>
<td>Sometimes absent</td>
<td>Finely papilllose with intertrabecular thickenings</td>
<td>Smooth</td>
<td>3-6 cell rows</td>
</tr>
<tr>
<td><em>Ph. tomentella</em></td>
<td>200-240</td>
<td>Smooth or porose, sometimes with scattered papillae</td>
<td>Smooth</td>
<td>Well developed</td>
<td>Finely papillose</td>
<td>Smooth</td>
<td>3-4 cell rows</td>
</tr>
</tbody>
</table>
Table 2. Endostome characters in *Philonotis*.

<table>
<thead>
<tr>
<th></th>
<th>Length (µm)</th>
<th>Upper third (PPL)</th>
<th>Base (PPL)</th>
<th>Upper third (IPL)</th>
<th>Base (IPL)</th>
<th>Number of cilia per cluster</th>
<th>Basal membrane</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ph. caespitosa</em></td>
<td>100-140</td>
<td>Papillose with simple papillae</td>
<td>Papillose with simple papillae</td>
<td>Papillose with simple papillae, sometimes bifurcate and disposed in rows</td>
<td>Smooth</td>
<td>2-3</td>
<td>4-6 cell rows</td>
</tr>
<tr>
<td><em>Ph. calcarea</em></td>
<td>150-200</td>
<td>Finely papillose with simple papillae</td>
<td>Smooth</td>
<td>Papillose with high and irregular papillae, sometimes branched or bifurcate</td>
<td>Finely papillose</td>
<td>3-4</td>
<td>3-5 cell rows</td>
</tr>
<tr>
<td><em>Ph. fontana</em></td>
<td>140-150</td>
<td>Rugulose</td>
<td>Rugulose</td>
<td>Papillose with simple papillae</td>
<td>Papillose with simple papillae</td>
<td>2-3</td>
<td>4-5 cell rows</td>
</tr>
<tr>
<td><em>Ph. rigida</em></td>
<td>220-330</td>
<td>Weakly papillose with simple and scattered papillae</td>
<td>Smooth</td>
<td>With papillose ridges</td>
<td>Smooth</td>
<td>3</td>
<td>3-5 cell rows</td>
</tr>
<tr>
<td><em>Ph. seriata</em></td>
<td>120-150</td>
<td>–</td>
<td>Smooth</td>
<td>Finely papillose with thinned areas in the walls</td>
<td>–</td>
<td>2-3</td>
<td>4-5 cell rows</td>
</tr>
<tr>
<td><em>Ph. tomentella</em></td>
<td>100-150</td>
<td>Finely papillose</td>
<td>Smooth</td>
<td>Finely papillose</td>
<td>Finely papillose</td>
<td>2</td>
<td>7 cell rows</td>
</tr>
</tbody>
</table>
Table 3. Spore characters in *Philonotis*.

<table>
<thead>
<tr>
<th>Shape</th>
<th>Size (μm)</th>
<th>Surface ornamentation</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ph. caespitosa</em></td>
<td>Subspherical to reniform</td>
<td>20-28</td>
</tr>
<tr>
<td><em>Ph. calcarea</em></td>
<td>Subspherical to reniform</td>
<td>24-26</td>
</tr>
<tr>
<td><em>Ph. fontana</em></td>
<td>Ovate to reniform</td>
<td>24-28</td>
</tr>
<tr>
<td><em>Ph. rigida</em></td>
<td>Subspherical to reniform</td>
<td>32-34</td>
</tr>
<tr>
<td><em>Ph. seriata</em></td>
<td>Spherical to reniform</td>
<td>26-30</td>
</tr>
<tr>
<td><em>Ph. tomentella</em></td>
<td>Reniform</td>
<td>24-26</td>
</tr>
</tbody>
</table>

groups of 2-3 (*Philonotis caespitosa, Ph. fontana, Ph. rigida, Ph. seriata, Ph. tomentella*) or 3-4 (*Philonotis calcarea*) cilia of the same or similar length as the segments. The endostomial PPL is usually less papillate and with lower papillae than the IPL, and also is crossed by lines that correspond to the trabeculae of the exostome teeth. The IPL is smooth (*Philonotis caespitosa, Ph. rigida*), papillate (*Philonotis calcarea, Ph. fontana, Ph. tomentella*) at the base and papillose or sometimes striate (*Philonotis rigida*) in the upper third. On the internal side, the endostome has lines that show the position of the cell walls that formed the inner peristomial layer. The cilia usually have the same ornamentation as the segments, and it is sometimes difficult to distinguish the differences between them. The basal membrane of the endostome is formed by 3-6(7) rows of variously polygonal, usually hyaline, papillose cells (Table 2).

The spores are reniform or subspherical, sometimes ovate (*Philonotis fontana*) or spherical (*Philonotis seriata*), brownish. The perine may consist of pilum-like processes (*Philonotis caespitosa, Ph. calcarea, Ph. rigida* and *Ph. tomentella*), bacula-like processes (*Philonotis seriata*) or may vary from granulae and verrucae to pila or clavae (*Philonotis fontana*). Spore size is quite consistent across the genus, though *Philonotis rigida* may have the largest of the group. However as Clarke (1979) stated, spore shape and size are the characters most affected by environmental conditions (Table 3).

This morphological study reveals significant differences in peristome structure between the six studied species. These are the development of the OPL median line and the papillosity of the exostome teeth, the papillosity of the endostomial segments, the number of cilia per cluster and the number of cell rows of the basal membrane. Regarding the spores, the character that mainly appears to be differential is the surface ornamentation. Although these are potentially the most accurate discriminatory characters between the studied species, further study and examination of all the European species are necessary to substantiate their taxonomic significance.

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REFERENCES


APPENDIX I. SELECTED SPECIMENS STUDIED

Philonotis caespitosa. SPAIN: Zamora, Arribes del Duero, arroyo que cruza la carretera entre Fermostoses y Pinilla de Fermostoses, Fernández Mendoza (MA-Musci 25426, MACB 80802).


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**Philonotis tomentella.** FINLAND: Ahvenanmaa, Saltvik, klippsprimor på Liby berg vid Kuggsund, Ranchen & Gotthberg (H 4105683). Enontekiö, Kilpisjärvi, Huuskonen (H 4106070). SPAIN: Ávila, Sierra de Gredos, Ros (MUB 15331).