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SPORE MORPHOLOGY OF SOME ORTHOTRICHACEAE ARN. SPECIES (BRYOPHYTA) FROM TURKEY

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Abstract

The spores of *Orthotrichum lyellii* Hook & Taylor, *O. speciosum* Nees, *O. affine* Schrad. ex Brid., *O. rupestre* Schleich. ex Schwagr., *O. anomalum* Hedw. and *O. cupulatum* Hoffm. ex Brid. showed the apertural region consists of a leptoma in their spores. Two spore types are characterized by their surface ornamentation, reflecting the species' taxonomic relationships. The spore shape of all the species is spheroid. The spore size ranged from 7 to 23 µm in the genus *Orthotrichum*. While the surface ornamentation is verrucate in *O. speciosum* and *O. affine*, it is gemmate in *O. lyellii*, *O. rupestre*, *O. anomalum* and *O. cupulatum*. The spore walls of the family Orthotrichaceae include sclerine (the distinction between exine and perine might be difficult to define) and intine. The examined moss species belong to two habitat types: corticolous and saxicolous. The taxonomic and ecological implications of the genus *Orthotrichum* were discussed on the basis of its spore morphology.

Introduction

The Orthotrichaceae Arn. family is mainly distributed in Europe, North America, Asia, and Africa. Species of Orthotrichaceae are tufted plants that grow on the trunks, branches and twigs of shrubs and trees, under sheltered or humid conditions, and on rocks and walls. The genus *Orthotrichum* Hedw. consists mainly of corticolous, epiphytic or saxicolous species of the Orthotrichaceae (Smith 2004). In the genus *Orthotrichum*, the spore size has been used for diagnostic purposes, but little is known about the potential value of spore ornamentation. This genus includes several difficult complexes in which these characters could be worth investigating (Medina *et al.* 2009). The capsules of *Orthotrichum* are immersed or emergent; the calyptrae range from glabrous to sparsely hairy; the basal parts of the leaves are not widened, concave or plicate; and the basal cells near the margins are not differentiated. In this study *Orthotrichum* genus is divided into three subgenera (Smith 2004).

Subgenus 1 **Gymnosporus** (Lindb. ex Braithw.) Limpr. Stomata superficial; mainly epiphytic. This subgenus is divided into two sections.

Section 1 *Leiocarpa* Mol. Leaves erect, flexuose when dry, acute to acuminate; margins usually recurved or revolute; cells papillose. Capsules immersed to exserted; spores 18 - 53 µm. Mainly in the southern Hemisphere. *Orthotrichum lyellii* is included in this section. *O. lyellii* is found on the trunks, branches and twigs of trees, often in less humid places than other species of *Orthotrichum*, and is rarely saxicolous.

Section 2 *Affinia* Schimp. Leaves erect, appressed when dry, acute to acuminate; margins usually recurved or revolute, cells in the upper part of leaf papillose, spores 13 - 30 µm. Mainly in the northern Hemisphere. *O. speciosum* and *O. affine* are included in this section. *O. speciosum* is

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frequently found on the trunks and branches of trees and shrubs and very rarely on rocks. *O. affine* is one of the most common corticolous mosses in Europe. It is found on the trunks, branches and twigs of shrubs and trees, especially *Betula*, *Fraxinus*, *Salix* and *Sambucus* in bright, sheltered or humid environments; on tree boles and exposed roots near streams and rivers; occasionally in quarries; and on rocks, walls and concrete. *O. affine* is extremely polymorphic regarding size and leaf morphology, seta length, capsule shape and calyptra hairiness, as well as exostome ornamentation (Vitt 1973, Smith 2004, Medina *et al.* 2009).

Subgenus 2 **Phaneroporum** Delogne. Leaves erect, appressed when dry, acute to acuminate; margins recurved or revolute; cells in the upper part of leaf papillose. Capsules emergent or exserted; stomata superficial; spores 9 - 28 µm. *O. rupestre* is located in this subgenus. *O. rupestre* is frequently found on dry, exposed, usually basic rocks by rivers and lakes; on stonework; on scree; and rarely on tree trunks and exposed roots.

Subgenus 3 **Orthotrichum.** Leaves erect, appressed when dry, obtuse to acute; margins usually recurved or revolute; cells smooth or papillose. Capsules immersed, emergent or exserted; stomata immersed; spores 9 - 19 µm. Mainly saxicolous species. *O. anomalum* and *O. cupulatum* are included in this subgenus. *O. anomalum* usually lives on exposed basic rocks, especially limestone, and on man-made substrates. *O. cupulatum* lives on flat limestone rocks and base-rich man-made habitats, such as wall tops and roofs and on limestone rocks in streams and by pools (Smith 2004).

Both the division of Orthotrichaceae and the separation of the genera were made according to their gametophytic and sporophytic characteristics. The spore characteristics are widely used in taxonomic analyses and descriptions of bryophytes. Not surprisingly, these characteristics have become models for the application of spore morphology in bryophyte systematics. Spore morphology has been of limited value in taxonomy; however, it has been useful in resolving taxonomic problems. It is also a potential source of information regarding the evolutionary processes, which may lead to the definition of biological or taxonomic boundaries (Carrion *et al*. 1995). In some recent papers (Sorsa and Koponen 1973, Vitt and Hamilton 1974, Boros and Járai-Komlódi 1975, Olesen and Mogensen 1978, Brown and Lemmon 1988, Blackmore and Barnes 1991, Gambardella *et al.* 1994, Carrion *et al.* 1995, Estebanez *et al.* 1997, Luizi-Ponzo and Barth 1998, 1999, Khoshravesh and Kazempour Osaloo 2007, Potoglu Erkara and Savaroglu 2007, Savaroglu *et al.* 2007, Savaroglu and Potoglu Erkara 2008, Medina *et al.* 2009, Aşçı *et al.* 2010, Caldeira *et al.* 2013), the intine structure and the spore external morphology have proven useful in characterizing moss taxa at the generic and specific levels. There is, however, still required research in this area.

The Turkish bryophyte spores were studied by Potoglu and Savaroglu (2007), Savaroglu *et al.* (2007), Savaroglu and Potoglu (2008), Aşçı *et al.* (2010). In the present investigation, the detailed spore morphological characteristics of some Orthotrichaceae species were studied with light microscopy (LM) and scanning electron microscopy (SEM). The aim was to characterize the spore morphology of six species of the Orthotrichaceae family to contribute in taxonomy, ecology and paleobotany.

Materials and Methods

The spore material was obtained from the Faculty of Science and Arts of Osmangazi University Herbarium. The external surface was observed using LM and SEM. The spores were prepared untreated with glycerin jelly on microscope slides (Wodehouse 1935), using the acetolysis method (Erdtman 1957) for LM. Measurements of the shortest and the largest diameters (in polar view), as well as the polar axis and the equatorial diameter (in equatorial view), were

taken in 25 randomly selected spores. The mean, standard deviation, standard error and range were calculated. The sclerine thickness and the largest length of the apertural region were based on 25 measurements, and the mean value is given. For scanning electron microscopy (SEM), the unacetolyzed spores were directly placed onto stubs. The stubs were then coated with carbon and gold in a vacuum evaporator to a total thickness of 7.5 - 15.0 nm and examined with a JEOL 5600LV scanning electron microscope at an accelerating voltage of 20 kV. The first exsiccate listed under the ‘‘Specimens examined’’ is the reference specimen, while the others are the comparisons. The terminology for spore morphology was proposed by Erdtman (1957), Boros and Járai-Komlódi (1975), Blackmore and Barnes (1991), Punt *et al.* (1994) and Kapp *et al.* (2000).

Results and Discussion

The sporoderm of the Orthotrichaceae consists of perine, exine and intine. The separation between the exine and perine may be difficult to define, so sclerine is a more appropriate term. The ornamentation is different in each genus, and it is sometimes possible to distinguish species based on these features. The apertural region consists of an aperture surrounded or not by one or more rings of ornamentation elements. The spores can be placed into two groups on the basis of their morphology: (1) The gemmate type and (2) the verrucate type. The range of measurements which is found in the reference specimens is in accordance with that of the comparison specimens, but the mean may be somewhat different. This difference reflects intraspecific variation. All of the spore morphometric data are presented in Tables 1-3.

Table 1. Morphometric data of the Orthotrichaceae spores (equatorial view).

Taxa	Measurements							
	P (μm)				E (μm)			
	R	$X \pm S_x$	S	V (%)	R	$X \pm S_x$	S	V (%)
Orthotrichum lyellii (N)	9.0-17.0	11.6 ± 0.4	2.2	4.9	12.0-19.0	15.8 ± 0.3	1.7	3
O. lyellii (A)	9.0-13.0	11.3 ± 0.2	1.1	1.2	13.0-16.0	14.7 ± 0.2	0.9	0.9
O. speciosum (N)	16.0-23.0	17.8 ± 0.4	1.8	3.1	17.0-22.0	18.7 ± 0.3	1.5	2.3
O. speciosum (A)	12.0-16.0	13.8 ± 0.2	1.1	1.2	14.0-19.0	16.4 ± 0.2	1.2	1.7
O. affine (N)	7.0-14.0	10.9 ± 0.4	1.9	3.8	10.0-18.0	15.0 ± 0.3	1.6	2.6
O. affine (A)	8.0-14.0	10.8 ± 0.4	1.8	3.1	12.0-17.0	14.6 ± 0.3	1.6	2.4
O. rupestre (N)	9.0-16.0	12.5 ± 0.4	2.0	4.2	14.0-19.0	17.1 ± 0.3	1.4	1.9
O. rupestre (A)	9.0-16.0	12.9 ± 0.5	2.4	5.8	14.0-19.0	17.2 ± 0.3	1.6	2.5
O. anomalum (N)	9.0-13.0	10.8 ± 0.2	1.1	1.3	12.0-18.0	14.7 ± 0.3	1.5	2.4
O. anomalum (A)	9.0-14.0	11.4 ± 0.3	1.4	1.9	12.0-18.0	15.1 ± 0.3	1.7	2.8
O. cupulatum (N)	11.0-15.0	12.6 ± 0.2	0.9	0.9	12.0-16.0	13.8 ± 0.2	1	1
O. cupulatum (A)	14.0-19.0	16.4 ± 0.2	1.2	1.5	16.0-22.0	18.8 ± 0.3	1.4	2

P: Polar axis**.** E: Equatorial diameter. R: Range. X: Mean. S: Standard deviation. S_x: Standard error. N: Non-acetolyzed spores. A: Acetolyzed spores. V: Variation.

The spore shape of all the species varied from almost spherical to angular. The spore size ranged from 10.8 (± 0.2) × 14.7 (± 0.3) μm in *O. anomalum* to 17.8 (± 0.4) × 18.7 (± 0.3) μm in *O. speciosum* (Table 1). Based on the exine surface ornamentation, two spore types can be recognized here. The spore type having a gemmate exine surface was found in four species, while

the type with a verrucate exine surface was observed in two species. The characteristics of these two spore types are described before in detail.

I. Gemmate exine surface. *Orthotrichum lyellii* Hook & Taylor, *O. rupestre* Schleich. ex Schwagr., *O. anomalum* Hedw. and *O. cupulatum* Hoffm. ex Brid. belong to this type. In these four species, the exine surface is similar to that of the former species with the exception that the gemmae are small, approximately 1 µm in diameter. Gemmae with smaller projections are scattered among them. The spores are small (ranging from 10.8 to 16.4 µm; Table 1), radially symmetrical, heteropolar and concave-convex in shape with a subcircular amb. The exine surface is ornamented by gemma-like elements. The apertural region consists of a rounded to subtriangular area that is bordered by a ring of gemma-like elements. The apertural region was interpreted to be a leptoma. The SEM shows irregularly shaped gemmate elements (Figs 1A-D, 4A-D, 5A-D, 6A-D).

II. Verrucate exine surface. *Orthotrichum speciosum* Nees and *O. affine* Schrad. ex Brid. belong to this type. In these two species, the exine surface is irregularly covered by scattered verrucae that are subpatterned by small granules on the surface. The spores are small (ranging from 10.8 to 17.8 µm; Table 1), bilaterally and sometimes radially symmetric to asymmetric, heteropolar and plane-convex to concave-convex in shape with a rounded to sub-rounded amb. The exine surface is ornamented by verruca-like elements (Figs 2A-D, 3A-D). The apertural region consists of a less resistant area in the majority of the taxa, and it was interpreted to be a leptoma. The verruca-like elements are larger and rarely dispersed; in these taxa, this field is

Table 2. Morphometric data of the Orthotrichaceae spores (polar view).

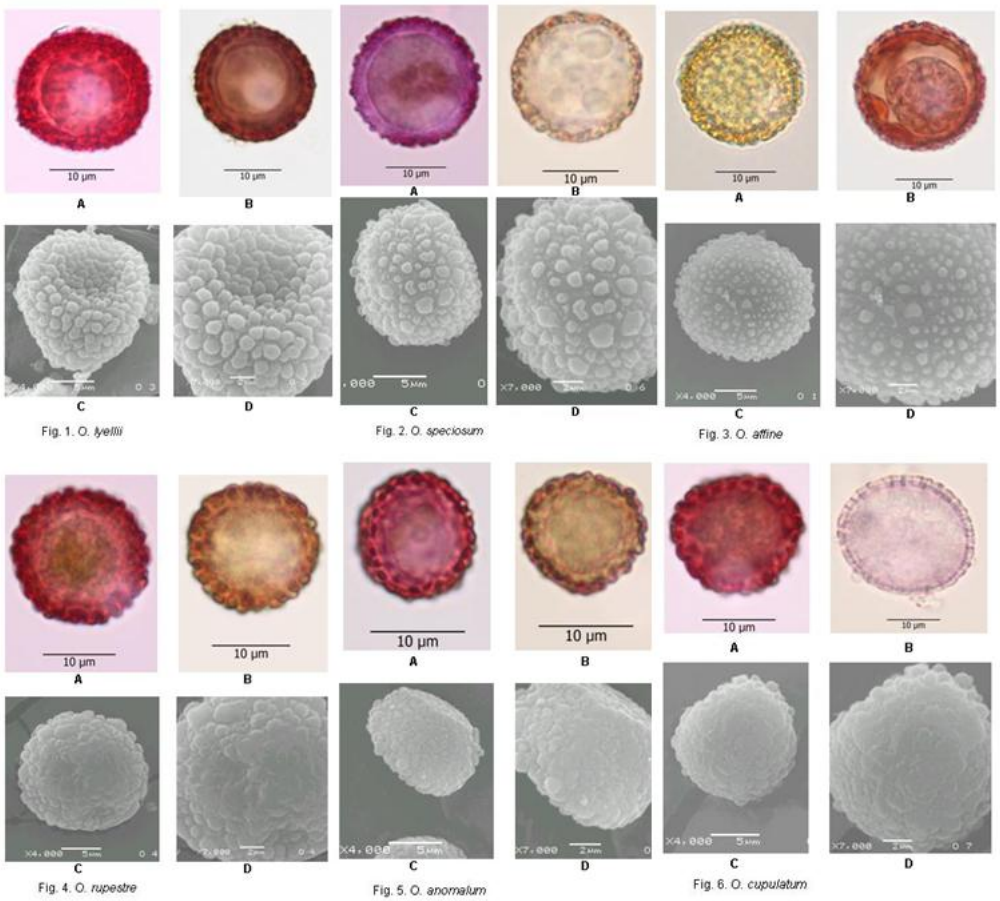
Taxa	Measurements							
	D_M (µm)				D_m (µm)			
	R	$X \pm S_x$	S	V (%)	R	$X \pm S_x$	S	V (%)
Orthotrichum lyellii (N)	14.0-18.0	16.4 ± 0.3	1.3	1.7	13.0-18.0	15.6 ± 0.3	1.4	1.9
O. lyellii (A)	14.0-18.0	16.1 ± 0.2	1.2	1.5	13.0-18.0	15.3 ± 0.3	1.4	1.9
O. speciosum (N)	15.0-26.0	23.4 ± 0.4	2.1	4.6	15.0-25.0	22.4 ± 0.4	1.9	3.9
O. speciosum (A)	13.0-22.0	16.9 ± 0.4	2	4.3	12.0-21.0	15.9 ± 0.4	2	4.2
O. affine (N)	11.0-19.0	15.6 ± 0.4	2.1	4.4	10.0-18.0	14.8 ± 0.4	2	4
O. affine (A)	14.0-18.0	15.9 ± 0.2	1.2	1.5	13.0-17.0	15.0 ± 0.2	1.2	1.4
O. rupestre (N)	13.0-19.0	15.8 ± 0.3	1.7	2.9	13.0-19.0	15.1 ± 0.4	1.8	3.1
O. rupestre (A)	15.0-19.0	17.4 ± 0.3	1.4	1.8	14.0-18.0	16.5 ± 0.3	1.4	1.9
O. anomalum (N)	9.0-15.0	12.2 ± 0.3	1.6	2.4	9.0-14.0	11.4 ± 0.3	1.5	2.1
O. anomalum (A)	11.0-17.0	13.9 ± 0.3	1.5	2.3	10.0-16.0	13.0 ± 0.3	1.4	2
O. cupulatum (N)	13.0-22.0	15.7 ± 0.4	1.9	3.9	12.0-21.0	14.6 ± 0.4	2	4
O. cupulatum (A)	13.0-22.0	16.9 ± 0.4	2	4.1	12.0-21.0	15.9 ± 0.4	2	4.1

D_M: Largest diameter. D_m: Smallest diameter. X: Mean. S: Standard deviation. S_x: Standard error. R: Range N: Non-acetolyzed spores. A: Acetolyzed spores. V: Variation.

evaluated as an aperture. The SEM studies are useful for spore type characterization but do not permit a clear differentiation of the investigated taxa. In addition to the occurrence of an aperture or a leptoma, the most important properties that facilitate the discrimination of these spores are the measurements of their largest diameter (Table 2). Some morphological variations were observed in the verrucate elements may occur in some taxa, but as far as we can see, these elements are not

a reliable method to distinguish between species because there is a great intraspecific variation in these characteristics.

The spore morphology of the species was based on the peristome morphology. The investigated taxa have short spores with four gemmate and two verrucate types of spore morphology. The examined spores were spheroidal. The spore morphology of the four gemmate species and the two verrucate species that were analyzed here has previously been reported (Boros *et al.* 1993, Kapp *et al.* 2000). The general spore morphology of most of these six species is the same as that which Boros *et al.* (1993) illustrated using light microscopy. The spore surface ornamentation is of diagnostic value in the identification of the six examined taxa, at least at the genus level and somewhat at the species level within the family. For instance, our present findings illustrate that these six species belong to only two spore types (gemmate and verrucate).



Figs 1 - 6. Spores of 1. *Orthotrichum lyellii*. 2. *O. speciosum*. 3. *O. affine*. 4. *O. rupestre*. 5. *O. anomalum*. 6. *O. cupulatum*. (A) proximal view (N; LM), (B) proximal view (A; LM), (C) distal surface (SEM), (D) close-up of spore (SEM).

The moss species that were examined are of two types with respect to their habitat: saxicolous species that inhabit rock surfaces and corticolous species that inhabit epiphytic surfaces. There is some correlation between the exine surface ornamentation and the vegetation substratum. While

the species with a gemmate spore ornamentation belong to saxicolous habitats (*Orthotrichum lyellii*, *O. rupestre*, *O. anomalum* and *O. cupulatum*), the other species with verrucate exine surfaces prefer corticolous habitats (*O. speciosum* and *O. affine*). The saxicolous members produce their sporophytes under conditions of high humidity and short-period sunlight, primarily during the winter season. It is noteworthy that the saxicolous species possess spores that are densely ornamented by exine elements, whereas the moisture-dependent species have spores that are loosely covered by subpatterned exine surfaces. Other morphological adaptations, including spore size, life forms and life strategies, that are related to the habitat conditions were reported in the Near and Middle East Bryophytes (Kürschner 2004, Khoshravesh and Kazempour Osaloo 2007).

Table 3. Morphometric data of the sclerine and apertural region of the Orthotrichaceae spores.

Taxa	Measurements	
	st (μm)	a (μm)
Orthotrichum lyellii (N)	0.9	7.3
O. lyellii (A)	0.9	7.1
O. speciosum (N)	1.0	12.3
O. speciosum (A)	1.0	7.4
O. affine (N)	0.9	6.6
O. affine (A)	0.9	6.5
O. rupestre (N)	0.9	8.0
O. rupestre (A)	0.9	7.0
O. anomalum (N)	0.9	6.3
O. anomalum (A)	0.9	8.3
O. cupulatum (N)	0.9	7.2
O. cupulatum (A)	1.0	7.4

st: Sclerine thickness. a: Largest length of the apertural region. N: Non-acetolyzed spores. A: Acetolyzed spores.

Furthermore, there is little correlation between the size and shape of the spores of the examined species and their habitats. All of the species possess small spores and common sporophytes that increase their chance of successful dispersal and of occupying new localities. These characteristics are related to a common strategy of drought resistance. This strategy is characterized by a longer life span, monoecy, regular sporophyte production, and the production of large quantities of small spores. This functional type is typical for saxicolous bryophytes and is used to compensate for the high mortality rate of the gametophytes, which is often caused by summer drought or erosion effects (Kürschner 2004). There is a predicted correlation between the spore morphology of the region with the relevant taxonomic groups and the ecological conditions. These types of investigations help us to predict the rarity, future ecological disturbance, and conservation of bryophytes.

The relatively simple spores of the moss family Orthotrichaceae do not offer many morphological characteristics that are useful for distinguishing between taxa. The ornamentation pattern of the spores is of taxonomic importance, as is evident from the distribution of the different spore types among the species (Luizi-Ponzo and Barth 1998, 1999, Khoshravesh and Kazempour Osaloo 2007, Potoglu and Savaroglu 2007, Savaroglu and Potoglu 2008). Spores of the gemmate and verrucate types are found in six species. The spores of some species of the Orthotrichaceae genera were described by Erdtman (1957), Boros and Járai-Komlódi (1975), Punt *et al.* (1994) and Kapp *et al.* (2000). Spore ornamentation and size are quite variable. The majority of species in *Orthotrichum* have spores that are coarsely papillose and range in size from 13 - 30 μm. All these

species except for *O. lyellii* have isosporous spores. *O. lyellii* is isosporous with spores of two size classes (Vitt 1973).

The results presented here are in conformity with those found by the above mentioned authors. However, diversities that have not previously been mentioned in the literature but were based on the present study include the surface ornamentation in *Orthotrichum lyellii*, *O. speciosum*, *O. affine*, *O. rupestre*, *O. anomalum* and *O. cupulatum*. There was sometimes some variability in the mean in the different specimens that were analyzed for each taxon, but the range of the measurements for the comparison specimens were always in accordance with that of the specimen reference. These results confirm those of Olesen and Mogensen (1978) and demonstrate the need to examine more than one specimen to characterize the spore size of a taxon.

Present study agrees with Sorsa and Koponen (1973), Vitt and Hamilton (1974), Boros and Járai-Komlódi (1975), Olesen and Mogensen (1978), Brown and Lemmon (1988), Blackmore and Barnes (1991), Estebanez *et al*. (1997), Luizi-Ponzo and Barth (1998, 1999), Khoshravesh and Kazempour (2007), Potoglu and Savaroglu (2007), Savaroglu *et al*. (2007), Savaroglu and Potoglu (2008), Medina *et al*. (2009), Aşçı *et al*. (2010), and Caldeira *et al*. (2013) that spore morphology in the Orthotrichaceae family and its relatives show distinctive properties that are important for taxonomic studies.

Specimens investigated

All specimens were from Turkey.

Orthotrichaceae Arn.

O. lyellii Hook. & Taylor B7 Eskişehir: Sündiken Mountains, Arikaya, *Pinus nigra* subsp. *pallasiana*-*Quercus cerris* var. *cerris* forest, 1200 m, 23.07.2000, on rock, Savaroglu 444.

O. speciosum Nees A2 Osmaneli (Bilecik): Mekece-Osmaneli road, *Pinus nigra*, 250 m, N 40°21'12.8", E 030°06'19.9", 01.05.2007, on *Quercus* sp., Savaroglu 1285.

Orthotrichum affine Schrad. ex Brid. A2 Osmaneli (Bilecik): Mekece, highland, 370 m, N 40°25'52.2", E 030°01'26.7", 01.05.2007, on *Quercus* sp., Savaroglu 1277.

O. rupestre Schleich. ex Schwagr. A1 Osmaneli (Bilecik): Vezirhan-Sarmaşik road, right side, forest road, 366 m, N 40°14'43.3", E 029°58'44.1", 15.05.2008, water edge, on rock, Savaroglu 1373.

O. anomalum Hedw. A2 Osmaneli (Bilecik): From Uyuk-Medetli, 167 m, N 40°16'14.4", E 030°06'00.9", 01.05.2006, on rock, Savaroglu 982.

O. cupulatum Hoffm. ex Brid. A2 Osmaneli (Bilecik): Buyuksusuz village, 581 m, N 40°16'54.6", E 030°10'06.9", 21.03.2007, on rock, Savaroglu 1205.

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