

Schistidium apocarpum complex (Grimmiaceae, Bryophyta) in the Baetic Mountain Ranges, southern Iberian Peninsula

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# Schistidium apocarpum complex (Grimmiaceae, Bryophyta) in the Baetic Mountain Ranges, southern Iberian Peninsula

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#### ABSTRACT

KEY WORDS Distribution, mosses, Schistidium, Spain, new combination. A morphological review of the *Schistidium apocarpum* complex (Grimmiaceae) in the Baetic Mountain Ranges (southern part of the Iberian Peninsula) was conducted. The study shows the presence of nine species in the territory. An identification key is provided, and the most relevant differentiating morphological characters of the species are described and analysed. Distribution patterns and important habitats for the species are discussed. *Schistidium apocarpum* (Hedw.) Bruch & Schimp. is excluded from the territory and the ranges of all the species are considerably expanded. A new combination is proposed, *Schistidium griseum* (Nees & Hornsch.) J.Guerra, comb. nov., stat. nov.

#### RÉSUMÉ

# Le complexe Schistidium apocarpum (Grimmiaceae, Bryophyta) dans les chaînes de montagnes Bétiques, au sud de la péninsule Ibérique.

MOTS CLÉS Distribution, mousses, Schistidium, Espagne, combinaison nouvelle. Une étude morphologique du complexe *Schistidium apocarpum* (Grimmiaceae) dans les chaînes de montagnes Bétiques (partie sud de la péninsule Ibérique) a été réalisée. L'étude montre la présence de neuf espèces sur le territoire. Une clé d'identification est fournie, et les caractères morphologiques distinctifs les plus pertinents de l'espèce sont décrits et analysés. Les schémas de distribution et les habitats importants pour l'espèce sont examinés. *Schistidium apocarpum* (Hedw.) Bruch & Schimp. est exclu du territoire et les aires de répartition de toutes les espèces sont considérablement élargies. Une nouvelle combinaison est proposée, *Schistidium griseum* (Nees & Hornsch.) J.Guerra, comb. nov., stat. nov.

# INTRODUCTION

The genus Schistidium Bruch & Schimp. includes around 110 species (Frey & Stech 2009), but the true number remains unknown, mainly due to the lack of studies in several regions of the globe. Moreover it is not only one of the most taxonomically difficult of moss genera, but also one of the least known and understood. The Schistidium apocarpum (Hedw.) Bruch & Schimp. complex was briefly defined by Blom (1996) as species with small spores and usually with an ability to form leaf hair-points. After the treatment of the S. apocarpum complex by Blom (1996), species concepts within this genus have changed significantly. In the light of Blom's research, numerous species of Schistidium have been described from various parts of the world, for example: Allen (2005), Blom & Darigo (2009), Blom & Lüth (2002), Blom et al. (2011), Blom et al. (2016), Feng et al. (2013), Guerra et al. (2019, 2020), Ignatova et al. (2009, 2016), McIntosh et al. (2015, 2017), Ochyra et al. (2003a), Ochyra & Afonina (1994, 2010), Ochyra & Bednarek-Ochyra (2011). Several authors have applied Blom's concepts to the genus, for example in Europe, Cortini-Pedrotti (2001) listed 13 species of the S. apocarpum complex for Italy, Ochyra et al. (2003b) recognized 16 species for Poland, and Smith (2004) cited 13 species for Britain and Ireland. Ignatov & Ignatova (2003) recognized seven species of the complex for Middle European Russia, and Suárez & Muñoz (2015) recognized 18 taxa in the Schistidium apocarpum complex in the Iberian Peninsula and Balearic Islands. On a broader scale, Hodgetts et al. (2020) included 53 species for Europe, Macaronesia and Cyprus, although Corley et al. (1981) had previously included only four species of this complex for Europe.

The studies of Goryunov et al. (2007) and Milyutina et al. (2007) using DNA data support a narrow species concept in Schistidium, and subsequent studies have shown that the ITS region is very effective in elucidating relationships within the genus (Ignatova et al. 2009; Milyutina et al. 2010; Ignatova et al. 2016; Hofbauer et al. 2016). Guerra et al. (2019, 2020) studied the affinities of taxa from southern Spain with samples from other areas, mainly Eurasia, by means of analysis based on ITS1-2 sequence data. The distinct status of some species was revealed with the help of molecular phylogenetic analysis (Fig. 1). In the light of these two papers S. pulchrum H.H.Blom was excluded from the flora of the Iberian Peninsula, and S. convergens J.Guerra & M.J.Cano and S. memnonium J.Guerra were described as new species. In addition, these papers provided a basis for the systematic placement of the nine species of the Schistidium apocarpum complex recognized in the southern part of the Iberian Peninsula (Fig. 1). Thus, S. confertum (Funck) Bruch & Schimp., S. convergens J.Guerra & M.J.Cano and S. flaccidum (De Not.) Ochyra were located in the Confertum-clade (Fig. 1); S. memnonium J.Guerra is located in the Frigidum-clade (Fig. 1); S. atrofus*cum* (Schimp.) Limpr., *S. brunnescens* Limpr., *S. crassipilum* H.H.Blom, *S. griseum* (Nees & Hornsch.) J.Guerra, comb. nov., stat. nov. and *S. helveticum* (Schkuhr) Deguchi are included in the Atrofuscum-clade (Fig. 1) (*sensu* Ignatova *et al.* 2009). These clades or groups of species (taxonomic category yet undefined) within the *Schistidium apocarpum* complex allow us to compare the species studied here by their phylogenetic relationship. On the other hand, this phylogenetic study shows the separation of two species, until now considered subspecies of *S. brunnescens*, and in consequence one of them elevated in this paper to the category of species: *S. griseum* comb. nov., stat. nov.(Fig. 1: Atrofuscum-clade bottom).

Some mountainous areas in the south of the Iberian Peninsula remain relatively poorly surveyed, as regards the distribution of several species of Schistidium. In the revision of Suárez & Muñoz (2015) for Flora Briofítica Ibérica, the southern provinces of Spain were poorly represented, to the extent that in some of them (for example Málaga and Murcia) not a single species of the genus was reported. The focus of the present study is to resolve remaining issues within the species of the Schistidium *apocarpum* complex. Our main objectives are: 1) to update the number of species that occur in the Baetic Mountain System; 2) to assist with the identification of the species by providing a dichotomous key with supporting photographs; 3) to study the most relevant differentiating morphological characters that allow the separation of these species; and 4) to update our knowledge of the habitat and distribution of the species in the Baetic Mountain Ranges. A brief synthesis of the distribution of the species in the Iberian Peninsula is presented.

# MATERIAL AND METHODS

#### STUDY AREA

The Baetic System (Sistema Bético) is one of the main mountain ranges in Spain. Located in the south and east of the Iberian Peninsula, it is also known as the Cordilleras Béticas (Baetic Mountain Ranges) or Montañas Béticas (Baetic Mountains). The Baetic Mountain is made up of multiple mountain ranges that extend from western Andalusia to the Murcia Region, southern Castile-La Mancha and Valencia. To the north, the Baetic System is separated from the Meseta Central and the Sierra Morena by the Guadalquivir basin. Generally the mountain ranges that are part of this system are aligned in a southwest-northeast direction. The best-known range of the Baetic System is the Sierra Nevada, which includes the summit of Mulhacén, the highest mountain in the Iberian Peninsula. The Rock of Gibraltar is also considered to be part of the Baetic System, but not the Cabo de Gata further east, which includes rocks of volcanic origin.

The Baetic System is sub-divided into a number of ranges (Fig. 2, of which the most important are: Penibaetic System (Sierra de las Nieves, Sierra de los Filabres, Sierra Nevada,

Fig. 1. — Maximum likelihood phylogenetic tree inferred for a sample of selected species of *Schistidium* Bruch & Schimp., from variation in the nuclear locus recovered for the nuclear ITS. Brach support values given are Bayesian posterior probabilities (Guerra *et al.* 2020, modified). Clades: Frigidum, Confertum, Apocarpum, Atrofuscum sensu Ignatova *et al.* (2009). Samples with a herbarium voucher come from the Baetic System.



KEY TO THE SPECIES OF THE SCHISTIDIUM APOCARPUM COMPLEX IN SOUTHERN SPAIN

1. Urn 0.7-0.9(1) mm long; peristome teeth 60-250(300) µm, entire to semi-perforated in upper and central part; 2. perichaetial leaves elliptical to lingulate; basal cells of leaves esinuose....... 1. S. atrofuscum (Schimp.) Limpr. Urn 1-1.5 mm long; peristome teeth 300-450 µm, perforated or cribrose, with perforations arranged in parallel lines; perichaetial leaves ovate-lanceolate to lanceolate; basal cells of leaves sinuose ..... Peristome absent or rudimentary; hair-point flattened, wide at insertion ..... 3. 9. S. flaccidum (De Not.) Ochyra Peristome present; hair point cylindrical or flattened, not wide at insertion ...... 4 Hair-point absent or rarely present as a very short and finely denticulate tip ...... 1. S. atrofuscum 4. Exothecial cells in central and lower part of the urn mostly long oblong and curved, without stomata ...... 6 5. Exothecial cells in central and lower part of the urn mostly rectangular, quadrate or oblong, with or without Lamina in upper and central part with 2-stratose or 3-stratose spots or striae, sometimes completely 2-stratose; 6. margins in upper and central part ranging from 2-stratose in 2-5 rows (or confluent with bistratose lamina) to Lamina in upper and central part 1-stratose or with 2-stratose spots or striae, never completely 2-stratose; Perichaetial leaves ovate-lanceolate, sometimes oblong, acute, not abruptly narrowed into the hyaline hair point; 7. Perichaetial leaves oblong, ovate-oblong or ovate-elliptical, acute to subobtuse, sometimes abruptly narrowed into the hyaline hair-point, leaves 1.5-2.7(3.2) mm long...... 6. S. memnonium J. Guerra 8. Peristome teeth perforated or cribrose, with perforations arranged in parallel lines; basal cells of leaves sinuose; 9. Peristome teeth entire or with few to several perforations in upper part, perforations not arranged in parallel lines; basal cells of leaves usually esinuose; plants usually brownish to dark olivaceous ..... 10. Hair-point flattened, usually strongly spinulose-denticulate; plants 0.50-1.0 cm long; urn 0.45-0.70 mm long..... Hair-point cylindrical, slightly spinulose, with short, erect to erect-patent spinulae; plants 1-3 cm long; urn 

Sierra de Baza, Sierra Espuña), Subbaetic System (Sierra de Grazalema, Sierra del Aljibe, Sierra de Huétor, Sierra de Loja, Sierra Arana, Sierras del Sur de Jaén) and Prebaetic System (Sierra de Mágina, Sierra de Cazorla, Sierra de Segura, Sierra de María, Sierra de Alcaraz, Sierra del Montgó). These mountain systems reach an altitude of 3479 m on Mulhacén peak. Rainfall varies from 500 to 2000 mm per year.

The main bedrock types are very diverse. Calcareous rocks (limestone, dolomite, marl limestone) are the most frequent. In the Penibaetic System, quartzites, mica schistes and gneiss are very abundant, and in the Subbaetic System, peridotites, sandstones and slate are usually abundant.

The Baetic System is home to a considerable number of Mediterranean forests (*Quercus rotundifolia* Lam., *Q. suber* L.,

*P. pinaster* Aiton), oak woodlands, broadleaf forests (*Quercus pyrenaica* Willd., *Q. faginea* Lam., *Acer granatense* Boiss.), and coniferous forests (*Abies pinsapo* Boiss., *Juniperus thurifera* L., *Pinus halepensis* Mill., *P. sylvestris* L., *P. nigra* J.F.Arnold), which vary with elevation, soils, bedrock, and topography. These different types of forests, together with the diversity of rocky substrates and rainfall, makes the studied area a hot spot for the diversity of *Schistidium* in the Iberian Peninsula. Open forests with sometimes sunny rocks are the most common habitat for species treated here.

# MORPHOLOGICAL STUDY

The *Schistidium apocarpum* group is the most complex and species-rich of the genus. The taxa are defined by a com-



FIG. 2. - Study area: the Baetic System and the sub-chains. Prebaetic Systems (red), Subbaetic System (yellow) and Penibaetic Systems (green).

bination of gametophyte and sporophyte characters. Of fundamental importance are the cell structure of the leaf lamina, the curvature of the leaf margins, the configuration of the hair-point, the size and shape of the urn, the exothecial cell pattern and the structure of the peristome (Blom 1996). The present study is based on a revision of 375 specimens from the south of the Iberian Peninsula, which are deposited in GDAC, MA, MGC and MUB (Selected specimens studied in Appendix 1). In addition, type material of Grimmia apocarpa var. grisea Nees & Hornsch. was studied from M Herbarium. The material was studied and described using standard anatomical and morphological methods applied within the Grimmiaceae (e.g. Blom 1996; Bednarek-Ochyra 2006). Microscopic examinations and measurements were taken with an Olympus-BH2 light microscope, using mature leaves from the portion of the stem just below the perichaetial leaves, while microphotographs were obtained with a Spot insight QE camera mounted on this microscope. Descriptions, measurements, key to the species and taxonomic notes are based exclusively on the specimens collected in the study area.

# RESULTS

ATROFUSCUM-CLADE

# 1. *Schistidium atrofuscum* (Schimp.) Limpr. (Fig. 3)

Die Laubmoose Deutschlands, Oesterreichs und der Schweiz 1: 713 (1889). — Grimmia atrofusca Schimp., Syn. musc. eur., ed. 2: 240 (1876).

Schistidium apocarpum var. atrofuscum (Schimp.) C.E.O. Jens. ex Weim., Förteckning öfer Skandinaviens Växter, Mossor ed. 2, 2: M28 (1937).

HABITAT. — Exposed calcareous rocks, from 1100 to 2000 m. Distribution: Figure 4. This species was known from very few provinces of Spain, and in the south it had only been cited from Jaén.

#### DESCRIPTION

Plants

Small, 0.7-1(1.5) cm long, forming dense and pulvinate tufts, jet-black. *Leaves* straight, erect, imbricate, triangular-ovate to ovate-lanceolate, obtuse to subacute,  $0.9-1.6 \times 0.3-0.5$  mm.



Fig. 3. – Schistidium atrofuscum (Schimp.) Limpr.: **A**, **B**, vegetative leaves; **C**, **D**, perichaetial leaves; **E**, apex of leaves; **F**, central and marginal laminal cells; **G**, apical laminal cells; **H**, basal laminal cells; **I**, transverse sections of lamina; **J**, peristome teeth; **K**, exothecial cells. (all from MUB 36532). Scale bar: A, B, 0.4 mm; C, D, 0.5 mm; E, 0.06 mm; F, G, 50 µm; H, 45 µm; I, 50 µm; J, 75 µm; K, 90 µm.



Fig. 4. – Distribution of Schistidium atrofuscum (Schimp.) Limpr. in the Baetic System.

# Hair-point

Absent or rarely present as a very short and finely denticulate tip, to 0.15 mm long, not very wide at insertion.

# Lamina

smooth, in upper and central part mostly 2-stratose to 1-stratose; margins plane in upper part, recurved in lower ½-⅔, 2-stratose in upper and central part.

#### Laminal cells

In upper and central part isodiametric to short oblong, not or slightly sinuose, mixed with oblate cells, 6-12  $\mu$ m long, basal cells esinuose, 15-40 × 8-10  $\mu$ m.

 $\begin{array}{l} \textit{Perichaetial leaves}\\ \textit{Elliptical to lingulate, 2-3.5}\times0.4\text{-}0.6 \text{ mm.} \end{array}$ 

# Urn shortly

oblong, sometimes cyathiform,  $0.7-0.9(1) \times 0.5-0.7$  mm, orange to yellowish.

# Exothecial cells

Predominantly rectangular, mixed with groups of short rectangular or isodiametric cells, stomata absent.

# Peristome teeth

 $60-250(300) \ \mu m$  long, sometimes very short to rudimentary, entire to semi-perforated in upper and central part, orangered to yellowish.

# Note

Similar in appearance to *S. helveticum* (Schkuhr) Deguchi, but smaller in size, peristome with rudimentary or very short teeth, with perforations not arranged in parallel lines, and basal laminal cells esinuose.

# 2. Schistidium brunnescens Limpr. (Fig. 5)

*Die Laubmoose Deutschlands, Oesterreichs und der Schweiz* 1:714 (1889).

HABITAT. — Exposed calcareous rocks, from 1650 to 1670 m. Distribution: Figure 6. This species was known from very few provinces of Spain and is here reported for the first time in the southern half of the country (Granada and Murcia provinces).

# DESCRIPTION

Plants

Small, (0.5)1-1,5 cm long, forming dense tufts, pale brown.

# Leaves

Straight, erect, imbricate, oblong, ovate to ovate-triangular, acute to acuminate,  $1.1-2.0 \times 0.3-0.4(0.7)$  mm.

# Hair-point

Usually present, rarely absent in some leaves, with scattered spinulae, (0)0.25-0.9 mm long.

# Lamina

Smooth, in upper and central part 1-stratose with occasional 2-stratose striae; margins plane or recurved in mid-leaf on one side, 1- to 2-stratose in upper and central part.

# Laminal cells

In upper and central part isodiametric to transversely oval, not or slightly sinuose, mixed with oblate cells, 6-9  $\mu$ m long, basal cells not or slightly sinuose, 20-40(45) × (6)8-10  $\mu$ m. *Perichaetial leaves* ovate to ovate-lanceolate, sometimes oblong, acute, not abruptly narrowed into the hyaline hair point, 2-2.8 × 0.6-0.8(0.9) mm.

# Urn

Broadly ovoid to shortly oblong,  $(0.6)0.7-0.9(1.2) \times 0.5-0.6(0.7)$  mm, yellow to orange-brown.

# Exothecial cells

Predominantly

Oblong, long and curved, mixed with patches of short rectangular cells, stomata absent.

# Peristome teeth

200-250(340) µm long, entire to semi-perforated in upper and central part, orange to orange-red.

# 3. *Schistidium crassipilum* H. H. Blom (Fig. 7)

Bryophytorum Bibliotheca 49: 224 (1996).

HABITAT. — Calcareous rocks in exposed or protected sites, rare on siliceous rocks or as an epiphyte on tree bark or stumps, from 650 to 1800 m. Distribution: Figure 8. Widespread throughout the Iberian Peninsula.

# DESCRIPTION

#### Plants

Small to medium-sized, (1.5)2-3.5 cm long, forming dense or loose tufts, usually brownish to dark olivaceous.

# Leaves

Straight or slightly curved, erect to patent, imbricate, triangular-ovate to ovate-lanceolate, sometimes elliptical, acute,  $1.5-3 \times 0.5-0.8$  mm.

# Hair-point

Cylindrical, somewhat flattened in lower part, finely to coarsely denticulate-spinulose, 0.1-1 mm long.

# Lamina

Smooth, sometime denticulate-papillose at margins in upper part, in upper and central part irregularly 2-stratose to 1-stratose with 2-stratose spots; *margins* recurved in lower  $\frac{1}{2}$ - $\frac{4}{5}$  of the leaf length on one side, 2-stratose in upper part.

# Laminal cells

In upper and central part isodiametric, not or slightly sinuose, (7)8-9  $\mu$ m long, basal cells rectangular to oblong, usually esinuose, (15)30-50 × 8-10(12)  $\mu$ m.

# Perichaetial leaves

Elliptical to ovate-lance olate, 3-3.9(4.2)  $\times$  (0.6)0.8-1.0 mm.

# Urn

Oblong-cylindrical,  $0.7-0.9(1.2) \times 0.5-0.7$  mm, red-brown to orange-brown.

# Exothecial cells

Predominantly oblong, mixed with groups of short rectangular or isodiametric cells, stomata absent or 1(2) rudimentary.



Fig. 5. – *Schistidium brunnescens* Limpr.: **A**, **B**, vegetative leaves; **C**, **D**, perichaetial leaves; **E**, **I**, apex of leaf; **F**, apical laminal cells; **G**, marginal laminal cells; **H**, basal laminal cells; **J**, central laminal cells; **K**, transverse sections of lamina; **L**, **M**, peristome teeth; **N**, **O**, exothecial cells. (all from MUB 11320). Scale bar: A, B, 0.3 mm; C, D, 0.5 mm; E, 0.07 mm; F, G, 70 µm; H, 64 µm; I, 60 µm; J, 65 µm; K, 0.08 mm; L, M, 80 µm; N, 75 µm; O, 50 µm.



Fig. 6. – Distribution of Schistidium brunnescens Limpr. (\*) and Schistidium convergens J.Guerra & M.J.Cano (•) in the Baetic System.

#### Peristome teeth

 $300\text{-}450~\mu\text{m}$  long, entire or with few to several perforations in upper part, not arranged in parallel lines, orange-red to orange-brown.

# Note

This species is probably the most variable taxon in the complex. Always without stomata, except one studied sample with rudimentary stomata present in the capsule.

# 4. *Schistidium helveticum* (Schkuhr) Deguchi (Fig. 9)

*Revue bryologique et lichénologique* n.s. 45: 434 (1979). — *Grimmia helvetica* Schkuhr, *Deutschland's kryptogamische Gewächse* 2 (2): 48 (1811).

Schistidium singarense (Schiffn.) Laz., Journal Institute of Botany Academy of Science of Ukraine 26-27: 205 (1938).

HABITAT. — Exposed calcareous rocks, rarely on tree bases (*Ul-mus*) or schists, from 680 to 2120 m. Distribution: Figure 10. Very common species in the Iberian Peninsula on limestone substrates.



Fig. 7. – Schistidium crassipilum H.H.Blom: A, B, vegetative leaves; C, D, perichaetial leaves; E, F, G, apex of leaves; H, K, central laminal cells; I, apical laminal cells; J, basal laminal cells; L, transverse sections of lamina; M, N, exothecial cells; O, peristome teeth. (all from MUB 14620). Scale bars: A, B, 0.5 mm; C, D, 0.7 mm; E, 0.12 mm; F, 0.24 mm; G, 0.7 mm; H, I, 0.16 mm; J, K, 35 µm; L, 60 µm; M, 75 µm; N, 50 µm; O, 100 µm.



Fig. 8. - Distribution of Schistidium crassipilum H.H.Blom in the Baetic System.

# Plants

Large to medium-sized or small, 1-3.5 cm long, forming dense tufts, jet-black to olivaceous or brownish.

# Leaves

More or less straight, erect, imbricate, lanceolate to ovatelanceolate, acute to subacute,  $(1.5)1.7-2.5 \times 0.4-0.6$  mm.

# Hair-point

Present, rarely absent, short, finely to coarsely spinulose, (0)0.1-0.2 mm long.

#### Lamina

Smooth, in upper and central part irregularly 2-stratose to 1-stratose; *margins* recurved along almost all its length except at the base, frequently 3- to 4-stratose in upper and central part.

# Laminal cells

In upper and central part isodiametric to oblong or oblate towards the margins, slightly to strongly sinuose, 12-18(20) µm long, basal cells thick-walled, sinuose,  $25-48 \times 6-12$  µm.

#### Perichaetial leaves

Ovate-lanceolate to lanceolate,  $2-4 \times 0.7$ -1.1 mm.



Fig. 9. – Schistidium helveticum (Schkuhr) Deguchi: A, B, vegetative leaves; C, D, perichaetial leaves; E, F, apex of leaves; G, apical laminal cells; H, J, central laminal cells; I, basal laminal cells; K, transverse sections of lamina; L, exothecial cells; M, N, peristome teeth. (all from MUB 56120). Scale bar: A, B, 0.4 mm; C, D, 0.5 mm; G, H, 70 µm; I, 45 µm; J, 35 µm; K, 70 µm; L, 75 µm; M, 100 µm; N, 30 µm.



Fig. 10. - Distribution of Schistidium helveticum (Schkuhr) Deguchi in the Baetic System.

# Urn

Oblong-cylindrical,  $1-1.5 \times 0.5-0.8$  mm, yellowish to orange-brown.

# Exothecial cells

Variable in shape and size, predominantly oblong, stomata absent.

# Peristome teeth

300-450  $\mu m$  long, perforated or cribrose, with perforations arranged in parallel lines, orange-red.

# Note

Very variable in size, depending on environmental conditions.

5. *Schistidium griseum* (Nees & Hornsch.) J.Guerra, comb. nov., stat. nov. (Fig. 11)

*Grimmia apocarpa* var. *grisea* Nees & Hornsch in Nees, Hornsch. & Sturm, *Bryologia Germanica* 2 (1): 91. XVI.4b. (1827). Lectotype



Fig. 11. – Schistidium griseum (Nees & Hornsch.) J.Guerra, comb. nov., stat. nov.: **A**, **B**, perichaetial leaves; **C**, **D**, vegetative leaves; **E**, **F**, apex of leaves; **G**, transverse sections of lamina; **H**, central laminal cells; **I**, basal laminal cells; **J**, **K**, exothecial cells; **L**, peristome teeth. (all from MUB 36519). Scale bar: A, B, 0.6 mm; C, D, 0.5 mm; E, 0.24 mm; F, 0.3 mm; G, 70 µm; H, 70 µm; I, 40 µm; J, 90 µm; K, 85 µm; L, 115 µm.



FIG. 12. — Distribution of Schistidium griseum (Nees & Hornsch.) J.Guerra, comb. nov., stat. nov. (\*) and Schistidium confertum (Funck) Bruch & Schimp. (•) in the Baetic System.

designated by Blom (1996): "*Grimmia apocarpa* var. *grisea* N. et H., *Bryologia Germanica* 2 p. ad saxa mont Pinif, Hb Funck" in M!

Schistidium brunnescens subsp. griseum (Nees & Hornsch.) H.H.Blom, Bryophytorum Bibliotheca 49: 218 (1996).

HABITAT. — Exposed calcareous rocks, around 1960 m. Distribution: Figure 12. In the Iberian Peninsula it is known from the Picos de Europa, Pyrenees and the Basque Country (Blom 1996; Heras & Infante 2002). The locality in Murcia (Moratalla, Sierra de Taibilla, *c*. 1960 m) is the southernmost in Europe.

# DESCRIPTION

Plants

Medium-sized, 1.5-2.5 cm long, forming dense to very dense tufts, blackish brown.

Leaves

Straight, erect, densely imbricate, ovate-lanceolate to ovatetriangular, acute to acuminate, sometimes with shoulders,  $(1.7)1.8-2.6(3.0) \times (0.4)0.5-0.7(0.9)$  mm.

# Hair-point

Very finely spinulose, (0)0.4-0.8(0.9) mm long.

#### Lamina smooth

In upper and central part with 2-stratose or 3-stratose spots or striae, sometimes completely 2-stratose; margins strongly recurved in lower  $\frac{1}{4}-\frac{1}{2}(\frac{2}{3})$  on one side, shortly recurved to plane on the opposite side, 2-stratose in 2-5 rows (or confluent with bistratose lamina) to 4-(5)-stratose in upper and central part.

#### Laminal cells

In upper and central part rounded to short oblong, slightly sinuose, often oblate,  $6-9(10) \mu m$  long, basal cells esinuose,  $(27)30-60 \times 10-15 \mu m$ .

#### Perichaetial leaves

Ovate-lanceolate, similar to vegetative leaves in shape, 2.8- $3.2 \times 0.7$ -0.8(0.9) mm.

# Urn

Broadly ovoid to oblong or cylindrical,  $0.7-0.9(1.1) \times 0.5-0.6(0.7)$  mm, orange to orange-brown.

#### Exothecial cells

Predominantly oblong, long and often curved, sometimes mixed with patches of short rectangular cells, stomata absent.

#### Peristome teeth

190-320(370) µm long, entire or with few narrow perforations in upper and central part, orange to orange-red.

#### Note

This species is similar to Schistidium brunnescens, from which it differs mainly in the stratification of the lamina, the width of the costa and the longer basal marginal cells of the vegetative leaves (cf. Guerra et al. 2020). The treatment of Blom (1996) for Schistidium brunnescens s.l. was perceptive, since morphological differences between the two taxa (S. brunnescens subsp. brunnescens and S. brunnescens subsp. griseum) are slight, and they have partly sympatric ranges. The morphological differences between the taxa can only be appreciated in the context of a review such as that carried out by Blom (1996). The rank of subspecies that he assigned to both taxa was surely a pragmatic solution, adequate in the context in which this study was carried out and in accord with the approach that Flatberg (1984) used in Sphagnum L.Hitherto they have been treated as conspecific taxa belonging to the S. atrofuscum group. In general, the rank of subspecies has been used to designate morphologically distinct and geographically isolated (allopatric) populations that are assumed to be genetically distinct or alternatively occupy different habitats (Kapadia 1963; O'Brien & Mayr 1991; Mallet 1995). That is, they are usually defined as requiring some geographic, ecological, and/or phylogenetic differentiation, beyond the morphological (Hamilton & Reichard 1992). Subspecies have been considered to be artificial

subdivisions of species or incipient species. However, with modern phylogenetic techniques, some subspecies may be found to represent genuine species (Burbrink *et al.* 2000). In the case of the two "subspecies" of *S. brunnescens*, there is no geographical isolation or appreciable difference in ecological behaviour; both grow on exposed limestone rocks at a similar elevation. Additionally, our molecular data show that the *S. griseum* comb. nov., stat. nov. specimens form a differentiated genetic lineage within the *S. brunnescens s.l.* clade (Fig. 1). This, together with the fact that both taxa can be differentiated morphologically, leads us to conclude that the subspecies *griseum* should be recognized at the species level.

FRIGIDUM-CLADE

# 6. *Schistidium memnonium* J.Guerra (Fig. 13)

#### Plant Biosystems (2020).

HABITAT. — Exposed and dry calcareous rocks, from 1300 to 1900 m. Distribution: Figure 14.

# Description

Plants

Medium-sized, sometimes small, 1.5-3.1 cm long, forming dense cushions or mats, brownish to blackish.

#### Leaves

Dense, erect, imbricate, ovate to ovate-triangular,  $1.5-2.7(3.2) \times 0.5-0.6(0.8)$  mm.

#### Hair-point

Straight, decurrent, dense and finely spinulose, to 0.6(0.9) mm long.

#### Lamina

Smooth, in lower part 1-stratose, occasionally with 2-stratose spots or short striae, in central and upper part varying from 1-stratose to partially 2-stratose in spots and striae; *margins* sometimes with very short papillae towards the apex near the hair-point, recurved from the base to near the apex on both sides, very rarely almost plane on one side, in lower part mostly 1-2-stratose in 1(2) rows, in upper and central part 2-3-stratose in 1-2 rows, not confluent with the bistratose lamina.

#### Laminal cells

In upper part isodiametric, rounded, ovate or elliptical, esinuose, (4)5-11  $\mu$ m long, basal cells occasionally sinuose, 10-45(50) × (4)5-7  $\mu$ m.

#### Perichaetial leaves

Oblong, ovate-oblong or ovate-elliptical, acute to subobtuse, sometime abruptly narrowed into the hyaline hair-point, similar in stratosity to vegetative leaves,  $2.8-3.4(3.5) \times 0.7-0.8(0.9)$  mm.



Fig. 13. — Schistidium memnonium J.Guerra: A, B, vegetative leaves; C, D, perichaetial leaves; E-G, apex of leaves; H, central laminal cells; I, basal laminal cells; J, transverse sections of lamina; K, L, exothecial cells; M, peristome teeth. (all from MUB 52209B). Scale bar: A, B, 0.8 mm; C, D, 0.7 mm; E, 0.24 mm; F, G, 0.15 mm; H, 30 µm; I, 45 µm; J, 70 µm; K, 75 µm; L, 70 µm; M, 92 µm.



Fig. 14. – Distribution of Schistidium memonium J.Guerra (\*) and Schistidium flaccidum (De Not.) Ochyra (•) in the Baetic System.

# Urn

Oblong to oblong-cylindrical,  $1.2-1.5(2) \times 0.4-0.5(0.6)$  mm, brown to reddish brown.

# Exothecial cells

In central part oblong to long rectangular or long obovate, in lower part around the junction with the seta long rectangular or long obovate, forming a regular pattern like a palisade, stomata absent.

#### Peristome teeth

 $(300)400-420 \ \mu m \ long$ , with 1-2 narrow slits along the median line in the upper part, margins irregular in outline, often with short lateral rami in central part, orange-brown.

# Note

This species is similar to *S. griseum* comb. nov., stat. nov. in habit, but differs in the stratification of the lamina and the shape of the perichaetial leaves.

# CONFERTUM-CLADE

7. *Schistidium confertum* (Funck) Bruch & Schimp. (Fig. 15)

Bryologia Europaea 3: 99 (1845). — Grimmia conferta Funck, Deutschlands Moose: 18 (1820).

Schistidium apocarpum var. confertum (Funck) H.Möller, Arkiv för Botanik 24 (2): 33 (1931).

HABITAT. — Exposed and dry siliceous rocks (gneiss, schist and mica schists), from 1650 to 3200 m. Distribution: Figure 12. In the Iberian Peninsula it is known from the Pyrenees, Cantabrian Mountains, Central System and Sierra Nevada.

# Description

#### Plants

Very small to small, 0.5-1 cm long, forming dense and pulvinate tufts, dark green to olive.

# Leaves

Straight, erect-patent, closely imbricate, ovate-lanceolate, ovate or triangular-ovate,  $0.6-1.4 \times (0.2)0.3-0.5(0.6)$  mm.

# Hair-point

Flattened, straight, not decurrent, not wide at insertion, usually strongly spinulose-denticulate, to 0.5 mm long.

# Lamina smooth

In upper and central part 1-stratose with 2-stratose spots; margins usually recurved on one side of leaf in central and lower part, 2- to 3-stratose in upper and central part.

# Laminal cells

In upper and central part isodiametric to oblong or oblate, not or slightly sinuose,  $(3.5)6.5-10.0 \ \mu m$  long, basal cells esinuose,  $7-30 \times 5-5(9) \ \mu m$ .

# Perichaetial leaves

Elliptical-lanceolate to ovate-lanceolate,  $(1.8)1.9-2.2 \times 0.4-0.6$  mm.

# Urn

Obovoid, ovoid or short cylindrical,  $0.45-0.70 \times 0.35-0.65$  mm, usually light yellow.

# Exothecial cells

In upper and central part irregular, rectangular or oblong towards the base, stomata small, (3)4-5 per urn.

# Peristome teeth

 $230-250(320) \mu m$  long, sometimes short, strongly perforated in central part with slits and small holes, orange-red.

# Note

This species is characterized by the combination of small size of the plants and vegetative leaves with hair-point strongly spinulose-denticulate.

# 8. *Schistidium convergens* J.Guerra & M.J.Cano (Fig. 16)

#### Nova Hedwigia 109: 72 (2019).

HABITAT. — Exposed and sunny rocks (gneiss, peridotites and mica schists), from 965 to 2520 m. Distribution: Figure 6. The species is known from northern Africa and southern Spain (Granada and Málaga provinces).

# DESCRIPTION

Plants

Small to medium-sized, 1-3 cm long, forming small tufts, olivaceous to brownish.

# Leaves

Straight, erect, imbricate, occasionally curved, ovate to triangular-ovate, acute,  $1.5-2.2 \times 0.3-0.4$  mm.

# Hair-point

Usually present, cylindrical, straight, not decurrent, slightly spinulose, with short, erect to erect-patent spinulae,  $0-250(300) \mu m$  long.

# Lamina

Smooth, slightly papillose at the apex, 1-stratose below, in central and upper part varying from 1-stratose to 2-stratose in spots and strips, to irregularly 2-3-stratose, margins recurved throughout, reaching apex on both sides, rarely plane on one side, 1- to 2-stratose in upper and central part.

# Laminal cells

Rounded, ovate or elliptical above, sometimes sinuose, in central part oblong and distinctly sinuose,  $(3.5)4-8 \times 4-5(8) \mu m$ , basal cells rectangular, esinuose,  $18-45(50) \times 5-7 \mu m$ .

#### Perichaetial leaves

Ovate-elliptical, markedly narrowed above the middle, 2.2- $2.3 \times 0.5$ -0.6 mm.

#### Urn

Oblong-cylindrical, slightly urceolate with age,  $1.0-1.2(1.3) \times 0.6-0.7$  mm, brown to red-brown.

# Exothecial cells

In upper and central part irregular, isodiametric, quadrate to short rectangular, sometimes oblate, stomata 2-4(5) per urn.

#### Peristome teeth

 $245-345 \mu m$  long, from entire to perforate with 1-2 narrow slits along median line in upper part, brown to orange-brown.

#### Note

Schistidium convergens is morphologically similar to S. crassipilum but there are numerous characters that distinguish the two species (Guerra *et al.* 2019). Schistidium crassipilum may have recurved leaf margins although the recurvature is



Fig. 15. – Schistidium confertum (Funck) Bruch & Schimp.: A, B, vegetative leaves; C, D, perichaetial leaves; E, F, apex of leaves; G, apical laminal cells; H, central laminal cells; I, basal laminal cells; J, alar laminal cells; K, transverse sections of lamina; L, exothecial cells; M, peristome teeth (all from MUB 57388). Scale bar: A-D, 0.3 mm; E, F, 0.16 mm; G, J, 35 µm; H, 40 µm; I, 37 µm; K, 50 µm; L, 70 µm; M, 110 µm.



Fig. 16. – Schistidium convergens J.Guerra & M.J.Cano: A, B, vegetative leaves; C, D, perichaetial leaves; E, F, apical laminal cells; G, H, apex of leaves; I, transverse sections of lamina; J, basal laminal cells; K, central laminal cells; L, exothecial cells; M, N, peristome teeth. (all from MUB 55721). Scale bar: A-D, 0.5 mm; E, F, 30 µm; G, H, 0.06 mm; I, 65 µm; J, 37 µm; K, 15 µm; L, 40 µm; M, N, 85 µm.



Fig. 17. – Schistidium flaccidum (De Not.) Ochyra: **A**, **B**, vegetative leaves; **C**, **D**, perichaetial leaves; **E**-**G**, apex of leaves; **H**, **I**, apical laminal cells; **J**, central laminal cells; **K**, transverse sections of lamina; **L**, exothecial cells; **M**, exothecial cells and stoma; **N**, peristome teeth. (all from MUB 56112). Scale bar: A, B, 0.4 mm; C, D, 0.7 mm; E, F, 0.19 mm; G, 0.12 mm; H-J, 25 µm; K, 50 µm; L, 70 µm; N, 25 µm; N, 120 µm.

usually limited to one side of the leaf. Exceptionally, *S. cras-sipilum* may have 1 or 2 stomata at the base of the capsule, but they are usually small, malformed, or inconspicuous. In addition, the exothecial cells in *S. crassipilum* are predominantly oblong, mixed with groups of short rectangular or isodiametric cells, rarely quadrate, a cellular pattern very different from *S. convergens* which has exothecial cells mostly quadrate.

# 9. *Schistidium flaccidum* (De Not.) Ochyra (Fig. 17)

Nova Hedwigia 48: 94 (1989). — Anictangium flaccidum De Not., Memorie della Reale Accademia delle Scienze di Torino 39: 254 (1836).

Schistidium pulvinatum var. flaccidum (De Not.) De Not., Syllabus Muscorum in Italia: 279 (1838).

HABITAT. — Gneiss and mica schists, usually in exposed and sunny places, from 1222 to 3115 m. Distribution: Figure 14. The species is known from various mountain ranges in the northern, central and southern parts of the Iberian Peninsula.

#### Description

#### Plants

Small to medium-sized, to 1.5 cm long, forming dense and pulvinate cushions, light green to brownish.

#### Leaves

Straight, erect, imbricate, ovate-lanceolate to triangular-ovate, acute,  $1.3-1.7(1.9) \times 0.5-0.7$  mm.

#### Hair-point

Flattened, wide at insertion, embracing a portion of the upper lamina, denticulate, flexuose, to 0.75 mm long.

#### Lamina

Smooth, 1-stratose occasionally with 2-stratose spots or short striae; *margins* recurved usually on both side of the leaf, 1- to 2-stratose in upper and central part.

# Laminal cells

In upper and central part isodiametric to short oblong or oblate, not or slightly sinuose, (5)7-10(12.5)  $\mu$ m long, basal cells esinuose, (17)30-50 × 7.5-10  $\mu$ m.

#### Perichaetial leaves

Ovate-lanceolate to oblong-lanceolate,  $(1.9)2-3 \times 0.6-0.8$  mm. Urn hemispherical, usually cyathiform,  $(0.6)0.7-0.9(1) \times 0.5-0.8$  mm, orange-brown to light yellowish.

# Exothecial cells

Irregular, predominantly rectangular in lower half of urn, stomata 3-6 per urn.

#### Peristome teeth

Absent or rudimentary, reduced to a short basal segment, orange.

#### Note

Unmistakable in its capsule usually without a peristome, and the distinctive hyaline hair-point, which is flattened, wide at insertion and flexuose.

# CONCLUSIONS

Nine species of *Schistidium* are found in the Baetic Mountain System. Of them, *Schistidium flaccidum*, *S. confertum* and *S. convergens* grow only on siliceous rocks and peridotites. Strictly basophilic are *S. atrofuscum*, *S. brunnescens*, *S. helveticum*, *S. memnonium* and *S. griseum* comb. nov., stat. nov. *Schistidium crassipilum* and *S. helveticum* rarely appear on acidic substrates, being very frequent only on calcareous or base-rich rocks.

The most frequent species are *S. helveticum* and *S. crassipilum*, since most of the mountainous territory is made up of limestone. The rarest species are *S. griseum* comb. nov., stat. nov. with only one locality in the Sierra de Taibilla (Murcia) and *S. convergens*, limited to some localities in the Sierra Nevada (Granada) and on the peridotite rocks of the Sierra de las Nieves (Málaga), here with only one known locality at present. *Schistidium flaccidum* and *S. confertum* are found only on acidic substrates (gneiss, mica schists, quartzite) in the Sierra Nevada and the Sierra de los Filabres, and they are not known from outside these mountain systems.

*Schistidium* species in the study area occur at an altitudinal range of 650 to 3200 m. The species that reach the highest altitudes are *S. confertum* and *S. flaccidum* on siliceous substrates (3115-3200 m in Sierra Nevada), and *S. atrofuscum* (2000 m in Sierra Nevada) and *S. helveticum* (2000 m in Revolcadores, Murcia; Sierra de la Sagra and Sierra de Baza, Granada, and 2120 m in Sierra de Gádor, Almería) on limestones.

*Schistidium apocarpum* has not been found in the territory at present; previous reports are probably due to confusion with *S. convergens* or *S. crassipilum*.

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#### APPENDIX

APPENDIX 1. — Selected specimens studied (only one sample for province).

#### Schistidium atrofuscum

MATERIAL EXAMINED. — Granada, Monachil, Sierra Nevada, alrededores de El Trevenque, 30SVG5803, 1740 m, roca metamórfica, 20.VI.2002, *Rams et al.* (MUB 24931). Jaén, Sierra de Segura, *c.* Segura de la Sierra, WH3039, 1100 m, 2.IV.1983, *Gil* (GDAC 22427). Málaga, Tolox, Sierra de las Nieves, vereda desde el puerto de los Pilones al Peñón de los Enamorados, 30SUF20236/62911, 1750 m, *Cabezudo et al.* (MUB 56928). Murcia, Moratalla, Sierra de Taibilla, peña de Moratalla, 38°4'N, 2°19'W, 1960 m, suelo entre rocas calizas, 12.VI.2011, *Cano* (MUB 36532).

#### Schistidium brunnescens

MATERIAL EXAMINED. — Granada, puerto del Pinar, entre La Puebla de Don Fadrique y Santiago de la Espada, WH4511, 1670 m, rocas calizas, 18.II.1998, *Guerra & Ros* (MUB 11320). Murcia, Moratalla, Sierra de Villafuerte, 38°8'N, 02°09'W, 30SWH7422, 1654 m, roca, 7.III.2003, *Cano* (MUB 16662).

#### Schistidium confertum

MATERIAL EXAMINED. — Almería, Gérgal, Sierra de Filabres, barranco del Negro, WG3922, 1650 m, roca ácida, 13.VI.1991, *García Zamora et al.* (MUB 9604). Granada, Sierra Nevada, Peñones de San Francisco, 2500 m, 37°6'N, 3°23'W, rocas silíceas (micaesquistos cuarcíticos), 1.VIII.2018, *Guerra* (MUB 57388).

#### Schistidium convergens

MATERIAL EXAMINED. — Almería, Bacares, Sierra de Filabres, barranco de Julián, WG4422, 1650 m, muro, 13.VI.1991, *García-Zamora & Ros* (MUB 9588). Granada, Güejar Sierra, Sierra Nevada, entre la estación de Maitena y el comienzo de la vereda de la Estrella, 37°08'N, 3°24'W, 1100 m, rocas silíceas, 2.VIII.2018, *Guerra* (MUB 57128). Málaga, Istán, cerro del Duque, pista desde el puerto de la Refriega al puerto del Algarrobo, 30SUF19377/55950, peridotitas, 900-1500 m, 29.VI.2017, *Cabezudo et al.* (MUB 56094).

#### Schistidium crassipilum

MATERIAL EXAMINED. — Albacete, Sierra de Alcaraz, río de las Espineras, 38°36'N, 02°22'W, 1300 m, tocón de *Ulmus montana*, *Guerra* (MUB 2240). Alicante, Jijona, Sierra de la Carrasqueta, cerca de Mas de Fondó, YH1978, 900 m, roca caliza, 25.II.1993, *Cano & Ros* (MUB 16489, MUB 9983). Cádiz, Grazalema, Puerto de las Palomas, 36°47'N, 5°22'W, 1216 m, roca caliza, 5.IV.2018, *Cano* (MUB 56737). Granada, Güejar Sierra, Sierra Nevada, bajada al castañar de Güejar Sierra desde el Dornajo, 37°8'N, 3°25'W, 1570 m, rocas silíceas, 20.VI.2018, *Guerra* (MUB 57384). Jaén, Sierra de Cazorla, cortijo de la Hortizuela, WH 1109, 700 m, roca caliza, 19.XII.1983, *Gil* (GDAC 39496). Málaga, Antequera, Torcal de Antequera, 36°57'N, 4°33'W, 1230 m, rocas calizas, 15.X.1978, *Oliva* (MUB 33835). Murcia, Moratalla, Rincón de los Huertos, 38°14'N, 02°02'W, 30SWH8233, 1280 m, roca caliza, 2.V.2002, *Cano* (MUB 14620).

#### Schistidium flaccidum

MATERIAL EXAMINED. — Almería, Sierra de los Filabres, arroyo Verruga, 37°13'N, 2°35'W, 1770 m, rocas silíceas, 9.V.2018, *Guerra et al.* (MUB 56902). Granada, Jérez del Marquesado, Sierra Nevada, subida al Postero Alto, margen izquierda del río Alhorí, 30SVG8109, 1500 m, 20.VI.2018, *Guerra* (MUB 56969).

#### Schistidium griseum comb. nov., stat. nov.

MATERIAL EXAMINED. — Murcia, Moratalla, Sierra de Taibilla, peña de Moratalla, 38°4'1"N, 2°19'44"W, 1960 m, roca caliza, 12.VI.2011, *Cano* (MUB 36519).

#### Schistidium helveticum

MATERIAL EXAMINED. — Albacete, reserva La Molata-Los Batanes, 1150 m, 38°40'N, 2°29'W, calizas, 17.V.2019, Guerra (MUB 58416). Alicante, Villena, Sierra de Salinas, barranco de los Pozos, XH7464, 950 m, roca caliza, 8/3/1993, Guerra & Cano (MUB 5587). Almería, Dalías, Sierra de Gádor, ca. Las Macetillas, 36°53'N, 02°48'W, 2120 m, rocas en un sumidero calizo, Guerra et al. (MUB 58318). Cádiz, Grazalema, Sierra del Pinar, 1500 m, rocas calizas expuestas, 3.VIII.2003, Guerra (MUB 15839). Granada, Puerto de la Mora, 30SVG52, 1350 m, calizas, 15.XII.1989, Varo (MUB 4301). Jaén, Sierra de Segura, Santiago de la Espada, Llanos de Hernán Perea, 37°58'N, 2°43'W, rocas calizas, 13.X.2017, Guerra (MUB 56095). Málaga, Parauta, Sierra de las Nieves, vereda del pinsapo de las Escaleretas, 1180 m, 30SUF1859, calizas, 6.VI.2018, Guerra et al. (MUB 56994). Murcia, Alhama de Murcia, Sierra Espuña, Pozos de la Nieve, 37°52'N, 1°34'W, 1457 m, roca caliza, 6.V.2018, Cano (MUB 56782).

#### Schistidium memnonium

MATERIAL EXAMINED. — Granada, Sierra de la Sagra, 37°57'N, 2°33'W, 1900 m, roca caliza, 12.II.2009, *Guerra* (MUB 52209B). Jaén, Sierra de Cazorla, Las Parcelas, loma de Cagasebo, WG0283, 1800 m, roca expuestas, IV.1996, *Ros & Monreal* (MUB 14560b). Málaga, Ronda, Sierra de las Nieves, entre el cortijo de Quejigales y el cerro de la Yedra, 30SUF1762, 1300 m, rocas calizas, 29.V.2018, *Cabezudo et al.* (MUB 56953).