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***Exormotheca martins-loussaoae* (Exormothecaceae, Hepaticae), a new species from Cape Verde**

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## Abstract

Former phylogenetic evidence for the genus *Exormotheca* revealed the existence of a distinct and monophyletic clade restricted to the oceanic archipelago of Cape Verde. During the fieldwork carried out in Cape Verde between 2016 and 2019, we found distinctive populations of *Exormotheca*. In this study, we aim to investigate the *Exormotheca pustulosa* complex and its relationship to other *Exormotheca* species that coexist in the same geographical areas, using morphological characteristics, and to present a formal description of a new *Exormotheca* species from Cape Verde Archipelago. A total of 60 specimens belonging to *Exormotheca* genus were examined. The specimens included samples, with broad taxonomic coverage of the *E. pustulosa* species, as well as from two phylogenetically close taxa *E. holstii*, and *E. welwitschii*. The characters studied were selected based on previous works that describe and distinguish species within the genus *Exormotheca*, and from our own observations. A new species, *Exormotheca martins-loussaoae* from Cape Verde is described. The new species can be recognized by the dark green color of the thallus and the almost entire dark purple scales, and the thallus surface having 6 – 9 regular rows with large conical air chambers, occupied by a thin assimilation tissue.

**Keywords:** Liverworts; Macaronesia; morphological analyses; endemic; *Exormotheca pustulosa*

## 42    **Introduction**

43    The genus *Exormotheca* Mitt. belongs to the family Exormothecaceae Söderström et al. 2016)  
44    and it is represented by five valid species (Long et al. 2016; Söderström et al. 2016).  
45    *Exormotheca bischlerae* Furuki & Higuchi (Furuki and Higuchi 2006), *Exormotheca*  
46    *brevipedunculata* (Kashyap) D.G.Long, Crandall-Stotler, L.L.Forrest & Villarreal (Long et al.  
47    2016), *Exormotheca holstii* Steph. (Stephani 1899), from China, India, and South Africa,  
48    respectively. The other two taxa are *Exormotheca welwitschii* Steph. (Stephani 1899) from  
49    Portugal, Spain, Algeria and Morocco (Ros et al. 2007), and *Exormotheca pustulosa* Mitt.  
50    (Mitten 1870), the most widespread species in the genus. The distribution range of *E. pustulosa*  
51    includes Macaronesia (the Azores, Madeira, Canary Islands and Cape Verde), the  
52    Mediterranean region (Portugal, Spain, France and Sicily), extending to tropical and  
53    southern/eastern Africa, the south Atlantic Island of Saint Helena and the western Indian island  
54    of La Réunion (Bischler-Causse et al. 2005; Ros et al. 2007; Hodgetts 2015). *Exormotheca*  
55    *pustulosa* shares geographical areas with *E. holstii* (South Africa) and *E. welwitschii*  
56    (Mediterranean region). *Exormotheca* species grow mainly on dry sandy and clay soils, on  
57    acidic cliffs and rock or sandstone outcrops, and on the rocky grasslands, which are generally  
58    only temporarily wet (Bischler-Causse et al. 2005; Perold 1999).

59    Recent phylogeographical evidence for the genus *Exormotheca* and in particular for the taxon  
60    *E. pustulosa* (Rodrigues et al. 2020) revealed the existence of three main groups. The Northern  
61    Macaronesia (Azores, Canary Islands and Madeira)/Western Mediterranean group, the South  
62    Africa/Saint Helena group, and another clade restricted to Cape Verde (Rodrigues et al. 2020).  
63    The genetically more separated population from La Réunion island appears to be basal to the  
64    clade comprising the northern Macaronesia/western Mediterranean and South Africa/Saint  
65    Helena groups, while the populations from Tanzania and Oman are sister to the monophyletic  
66    clade restricted to Cape Verde clade (Rodrigues et al. 2020). However, we assume that further

studies, including fieldwork in southern and eastern Africa is necessary. Based on the cpDNA and nDNA datasets, Macaronesia seems to have been colonized during the Pleistocene at least twice by two independent lineages of *E. pustulosa*. One of the lineages probably originated in SE Africa and dispersed across the northern Macaronesian archipelagos, while the other, with an origin in the Middle East/east Africa, colonized and remained in Cape Verde (Rodrigues et al. 2020). The cpDNA and nDNA median-joining networks revealed different and exclusive haplotypes for the Cape Verde group, foreseeing that further morphological taxonomic research to address species delimitations and relationships within *E. pustulosa* were necessary (Rodrigues et al. 2020). In this study, we aim to investigate (1) the *Exormotheca pustulosa* complex in Macaronesia, focusing on, mainland Portugal, and southern/eastern Africa, and its relationship to other *Exormotheca* species that coexist in the same geographical areas, using morphological characteristics, and (2) to present a formal description of a new *Exormotheca* species from Cape Verde Archipelago.

## Material and methods

A total of 60 specimens belonging to the genus *Exormotheca* were studied, 29 specimens from herbarium (LISU, E, PRE and Dirske private collection), and 31 specimens collected in the field (Azores, Cape Verde, Madeira, mainland Portugal and South Africa), between 2016-2019. The sampling covered a large proportion of the distribution range of *E. pustulosa*, but it was not possible to include samples from Morocco, France, mainland Spain or Sicily (Italy), as mentioned in Rodrigues et al. (2020). In turn, *E. holstii* (four samples) and *E. welwitschii* (three) were considered in the present study due to their phylogenetic proximity to the taxon of interest (Supplementary Table 1). The 37 *E. pustulosa* samples were mainly from the Macaronesia region: the Azores (one specimen; Faial island), Canary Islands (eight specimens; Gran Canaria, El Hierro, La Gomera, La Palma and Tenerife islands), Madeira (six specimens;

Madeira and Porto Santo islands) and other regions as Kenya (one specimen), La Réunion island (one specimen), mainland Portugal (four specimens), Oman (one specimen), South Africa (ten specimens), Saint Helena island (four specimens) and Tanzania (one specimen). The 16 specimens from Cape Verde (Santo Antão, São Nicolau, and Fogo islands) correspond to the new undescribed species. Voucher specimens of the new species described in this paper are deposited at LISU and TFC.

The specimens' observations and measurements were carried out by stereoscopic microscope (Olympus SZ40) and light microscopy (Olympus BX 51). The characters studied were carefully selected based on previous studies that describe and distinguish species within the genus *Exormotheca* (Perold 1999; Bischler-Causse et al. 2005; Frey et al. 2006), and from our own observations. Twenty-one quantitative and three qualitative characters were studied for the gametophyte. Representative spores of the *Exormotheca* species from Madeira and Cape Verde were observed through Scanning Electron Microscopy (SEM). However, due to an insufficient sample size, the sporophyte characters were excluded from the subsequent statistical analyses.

Descriptive statistics (mean and SD) was calculated for all quantitative characters. The morphological variation in the 16 diagnostic quantitative characters was evaluated by analyses of variance (ANOVA). Each single diagnostic quantitative character of the four species was tested followed by a post-hoc Tukey test of multiple comparisons analysis. The most representative characters for each species were represented in the form of beanplot graphs (Kampstra 2008). The analyses were carried out with R v.3.6.3 (R Core Team 2020).

## Results

*Exormotheca martins-loussaoae* Sim-Sim, A.Martins, J.Patiño & C.A.Garcia, *sp. nov.*

(Figures 1–3)

**Type:** Cape Verde, São Nicolau: road to Hortelão, lower limit of the Monte Gordo Natural Park, 16°36'59"N, 24°20'30"W, 847 m a.s.l., 19.11.2017, *M. Sim-Sim & C.A. Garcia* SN16 (holotype LISU266756!; isotype TFC).

**Paratypes:** São Nicolau: near Igreja house. Trail to ribeira dos Calhaus, 16°37'42"N, 24°21'20"W, 1025 m a.s.l., 18.11.2017, *M. Sim-Sim & C.A. Garcia* SN012 (LISU266755); Santo Antão: road to Pico da Cruz, 17°6'16"N, 25°3'0"W, 1304 m a.s.l., 14.09.2019, *M. Sim-Sim, C.A. Garcia & A. Martins* SA16 (LISU).

[Figure 1–3 near here]

**Description:** Plants in small to large, crowded patches, thalli small, dark green with numerous prominent conical evaginations of the dorsal epidermis, opening by air pores on the apices; margins with dark purple imbricate scales extending slightly above thallus margins when wet and strongly incurved over dorsal face when dry, giving a dark appearance to the thallus (Figure 1). Branches simple or dichotomous furcate, linear to ligulate, 5 – 10 mm long, 1.25 – 3 mm wide, 950 – 1300 µm thick at median region, in section 1.3 – 2.3 times wider than thick, thallus flat with margins quite obtuse, covered by air chamber rows; flanks obliquely upward, covered by imbricate scales.

Dorsal epidermis cells hyaline, unistratose, 45 – 77.5 x 17.5 – 40 µm, thin walled, with conical protuberances of air chambers 247.5 – 520 µm high and 250 – 375 µm wide, in 6 – 9 regular rows along the thallus surface; air pores simple round at the top of the air chamber, 50 – 60 µm wide, surrounded by 2 rings of thin-walled cells, the innermost of 8 – 10 cells, 20 – 30 x 10 – 12 µm (Figure 1). Assimilation tissue, 137.5 – 195 µm thick, occupying +/- ½ of air chambers, consisting of uniseriate filaments containing cells with numerous chloroplast, 5(6) cells free, 27.5 – 46.8 x 21 – 25 µm and one apical conical cell, 45 – 50 x 15 – 25 µm (Figure 2); storage tissue +/- 700 µm thick, with polygonal cells irregular in size 54 – 107.5 x 35 – 85 µm, containing a brown granular oil bodies 24 – 50 x 17.5 – 40 µm, rhizoids numerous

translucent and tuberculate arising from ventral epidermis. Scales oblong, 850 – 1400 x 550 – 1150  $\mu$ m, with 1 or 2 appendages at margins, dark purple, frequently with 1 – 2 hyaline marginal cells rows, projecting above thallus margins, mid cells 106 – 150 x 26–35  $\mu$ m becoming smaller at margins, lacking oil cells (Figure 2).

Monoicous. Androecia in 2 – 3 rows along thallus midline, close to (distal or proximal) female receptacle, with antheridia sunken in a shallow groove and their necks protruding. Gynoecia receptacles close to bifurcation of 2 terminal branches, sessile when young, at maturity on a stalk, up to 13 mm, 500  $\mu$ m diameter; carpocephalum with air chambers not protuberant, opening by simple air pores and hammer-like in shape, up to 3 mm across, with 2 capsules exerted laterally (Figure 1). Sporophyte with short seta 1200 x 800  $\mu$ m, capsule globose, wall unistratose, with semi-annular thickenings to L-shaped thickenings on radial and transverse walls extending to tangential walls, dehiscent by 4 – 5 irregular valves. Spores up to 75  $\mu$ m diameter, triangular-globular, distal face rounded, with +/- up to 35 crowded irregular hollow papillae, 10  $\mu$ m high to 15  $\mu$ m wide, walls of papillae to 1  $\mu$ m composed of adjoining granules stalked into pillars up to 2.5  $\mu$ m high exposed when wall is broken (Figure 3); proximal face with vestigial triradiate mark, finely granulose and wing absent. Elaters up to 200 x 15  $\mu$ m, trispiral.

**Diagnosis:** The species can be distinguished from *E. pustulosa* by the dark green color of the thallus and the almost entire dark purple scales, giving a blackish appearance to the thallus when dry; by its larger conical air chamber which are basal +/- 1/2 occupied by assimilation tissue; by the larger cells of the storage tissue and oil bodies; by both the larger ventral scales and mid cells of ventral scales; and by the larger spores.

**Distribution and habitat:** *Exormotheca martins-loussaoae* was found between 165–1480 m a.s.l on volcanic rocky slopes in mesic to dry areas, sometimes close to trails, in three Cape Verde Islands: Fogo, Santo Antão and São Nicolau (Figure 4). This species grows in small

fissures and crevices of basaltic rocks (Goth et al. 2016) in association with other bryophyte species such as *Bartramia laevisphaera* (Taylor) Müll.Hal., *Bryum argenteum* Hedw., *Bryum dichotomum* Hedw., *Grimmia laevigata* (Brid.) Brid., *Grimmia lisae* De Not., *Lunularia cruciata* (L.) Dumort. ex Lindb., *Mannia androgyna* (L.) A.Evans, *Plagiochasma rupestre* (J.R.Forst. & G.Forst.) Steph., and *Ptychomitrium nigrescens* (Kunze) Wijk & Margad.

**[Figure 4 near here]**

The new species is frequent in São Nicolau, occasionally with sporophytes like in the type locality, where large populations were found. The site was a basaltic steep slope exposed to the ocean on the northern side of the island. The type *Exormotheca* population occurs in small crevices and concavities with a thin layer of soil forming pure mats or with a small admixture of *Bryum argenteum* Hedw. and *Mannia androgyna* (L.) A.Evans. The new species was associated with a new species endemic to São Nicolau, *Campanula fransinea* Gardère (Gardère et al. 2021), with the pteridophyte *Cosentinia vellea* (Aiton) Tod., and with *Umbilicus* sp. (Neto et al. 2020).

**Etymology:** The new liverwort is named in honor of Maria Amélia Martins-Loução, an eminent botanist and ecologist, retired Full Professor at the University of Lisbon, Faculty of Sciences and former Director of the Lisbon Botanic Garden

## Discussion

Previous phylogeographical evidence in the genus *Exormotheca* revealed a distinct and monophyletic group for the Cape Verde (Rodrigues et al. 2020). Additionally, the reassessment of morphological characters allowed us to demonstrate that the Cape Verde clade should be formally distinguished at the species level. All four *Exormotheca* studied species can be distinguished morphologically based on a combination of characters summarized in Table 1. The analysis of the gametophyte quantitative characters revealed a large variation among



species. Sixteen quantitative characters exhibited statistical differences for the four studied species (Table 1). The morphometric analyses performed (Figures 1–3) showed that, despite the similarities of the new *Exormotheca* species with *E. pustulosa*, discrimination is possible using a combination of traits. In addition, the southern/eastern African (La Réunion island, Oman, Saint Helena, South Africa, Tanzania) and the northern Macaronesia/western Mediterranean group fit in the description of *E. pustulosa*.

**[Table 1 near here]**

The small thallus, the purple oblong to rounded scales, with 1 or 2 filiform appendages, the gynoecia receptacle with a long stalk, and the long and trispiral elaters (Perold 1999), placed *E. martins-loussaoae* in the subgenus *Exormotheca* Mitt. together with *E. pustulosa* (Söderström et al. 2016). The new species can be recognized by the dark green color of the thallus and the almost entire dark purple scales (Figures 1–2). Moreover, the thallus surface has 6 – 9 regular rows (Figure 1, Table 1, Supplementary Figure 1), with large conical air chambers 247.5 – 520 µm high (Figures 1–2, Table 1, Supplementary Figure 1), occupied by a thin assimilation tissue of 137.5 – 195 µm (Figure 2, Table 1, Supplementary Figure 1). The widespread *E. pustulosa* share with the new species the cells size of epidermal and the length of the chlorophyllose filaments cells, as well as the thickness of the storage tissue (Table 1, Supplementary Figure 1). Nevertheless, *E. martins-loussaoae* differs from *E. pustulosa* by the darker color of the thallus and scales, by the larger conical air chambers with thin assimilation tissue, as well as the larger length of the storage tissue cells and oil bodies. Additionally, the number of cells surrounding the air pores is smaller, while the spore diameter, the ventral scales and the length of their mid cells are larger in *E. martins-loussaoae* than in *E. pustulosa* (Table 1, Supplementary Figure 1).

*Exormotheca holstii* and *E. welwitchii* belong to subgenus *Corbierella* (Douin et Trab.) Schiffn. (Söderström et al. 2016) and are clearly distinct from the new species. The endemic taxon to South Africa, *E. holstii*, share with the new species the length of the storage tissue cells

and size of ventral scales cells (Table 1, Supplementary Figure 1). It is distinguished from *E. martins-loussaoae* by the glaucous color of the thallus, by the larger conical air chambers in rows and thickness of the assimilation tissue, as well as larger epidermal cells and higher number of cells surrounding air pores. Furthermore, the length of the chlorophyllose filaments cells, the thickness of the storage tissue, oil bodies and ventral scales are larger (Table 1, Supplementary Figure 1).

*Exormotheca welwitchii* known from Portugal, Spain, Algeria and Morocco can be distinguished from *E. martins-loussaoae* by the glaucous color of the thallus and hyaline scales, by its larger pustular air chambers in rows and thickness of the assimilation tissue, larger epidermal cells and higher number of cells surrounding the air pores, as well as thinner storage tissue and smaller oil bodies (Table 1, Supplementary Figure 1). Both species share the length of chlorophyllose filaments cells, and the length of storage tissue cells (Table 1, Supplementary Figure 1).

*Exormotheca martins-loussaoae* is a new species endemic from the Cape Verde archipelago in Fogo, Santo Antão and São Nicolau islands. In São Nicolau, this species can be found in the Monte Gordo region (type locality) together with a new vascular plant endemic to this region, *Campanula fransinea* (Gardère et al. 2021), the pteridophyte *Cosentinia vellea* (Aiton) Tod., and *Umbilicus* sp. (Neto et al. 2020).

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## 243 **Disclosure statement**

244 The authors declare that they have no conflict of interests.

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## 262 **References**

263 Bischler-Causse H, Gradstein SR, Jovet-Ast S, Long DG Allen NS. 2005. Marchantiidae. Fl.  
264 Neotrop. Monogr. 97:1–262.

265 Frey W, Frahm J-P, Fischer E, Lobin W. 2006. The liverworts, mosses and ferns of Europe.  
 266 Colchester: Harley Books.

267 Furuki T, Higuchi M. 2006. A New Species of *Exormotheca* (Exormothecaceae, Hepaticae)  
 268 from China. *Cryptogam. Bryol.* 27(1):97–102.

269 Gardère ML, Florence J, Muller S, Savriama Y, Dubuisson J.Y. 2021. *Codonographia*  
 270 *Gorgonum*, or the description of a pleiad of bellflowers (*Campanula*, Campanulaceae)  
 271 from the Cabo Verde archipelago. *Candollea.* 76(1):13–40.

272 Goth B, Cunha L, Ramos A. 2016. Le géopatrimoine de l'île de São Nicolau (Cap-Vert).  
 273 Inventaire et stratégie de valorisation. *Dynamiques environnementales.* 37:114–129.

274 Hodgetts NG. 2015. Checklist and country status of European bryophytes – towards a new Red  
 275 List for Europe. In: Irish wildlife manuals, No. 84. Dublin: National Parks and Wildlife  
 276 Service, Department of the Arts, Heritage and the Gaeltacht.

277 Kampstra P. 2008. Beanplot: A boxplot alternative for visual comparison of distributions.  
 278 *Journal of Statistical Software.* 28:1–9.

279 Long DG, Forrest LL, Villarreal JC, Crandall-Stotler BJ. 2016. Taxonomic changes in  
 280 Marchantiaceae, Corsiniaceae and Cleveaceae (Marchantiidae, Marchantiophyta).  
 281 *Phytotaxa.* 252:077–080.

282 Mitten W. 1870. Hepaticae. In: Godman F, editors. Natural History of the Azores, or Western  
 283 Islands. John Van Voorst. p. 316 –328. London.

284 Neto C, Costa JC, Figueiredo A, Capelo J, Gomes I, Vitória S, Semedo JM, Lopes A, Dinis H,  
 285 Correia E, Duarte MC, Romeiras MM. 2020. The Role of Climate and Topography in  
 286 Shaping the Diversity of Plant Communities in Cabo Verde Islands. *Divers.* 12(2):80.

287 Perold SM. 1999. Flora of Southern Africa Hepatophyta. Part 1. Marchantiopsida, Fascicle 1:  
 288 Marchantiidae. Pretoria: National Botanical institute.

- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.
- Rodrigues ASB, Martins A, Garcia CA, Sérgio C, Porley R, Fontinha S, González-Mancebo JM, Gabriel R, Phephu N, Van Rooy J, Dirkse G, Long D, Stech M, Patiño J, Sim-Sim M. 2020. Climate-driven vicariance and long-distance dispersal explain the Rand Flora pattern in the liverwort *Exormotheca pustulosa* (Marchantiophyta). Biol. J. Linn. Soc. Lond. 130(3):480–496.
- Ros RM, Mazimpaka V, Abou-Salam U, Aleffi M, Blockeel TL, Brugués M, Cano MJ, Cros RM, Dia MG, Dirkse GM, El Saadawi W, Erdağ A, Ganeva A, González-Mancebo JM, Herrnstadt I, Khalil K, Kürschner H, Lanfranco E, Losada-Lima A, Refai MS, Rodríguez-Núñez S, Sabovljević M, Sérgio C, Shabbara H, Sim-Sim M, Söderström L. 2007. Hepatics and Anthocerotes of the Mediterranean, an annotated checklist. Cryptogam. Bryol. 28:351–437.
- Söderström L, Hagborg A, von Konrat M, Bartholomew-Began S, Bell D, Briscoe L, Brown E, Cargill DC, Costa DP, Crandall-Stotler BJ, Cooper ED, Dauphin G, Engel JJ, Feldberg K, Glenny D, Gradstein SR, He X, Heinrichs J, Hentschel J, Ilkiu-Borges AL, Katagiri T, Konstantinova NA, Larraín J, Long DG, Nebel M, Pócs T, Puche F, Reiner-Drehwald E, Renner MAM, Sass-Gyarmati A, Schäfer-Verwimp A, Moragues JGS, Stotler RE, Sukkharak P, Thiers BM, Uribe J, Vána J, Villarreal JC, Wigginton M, Zhang L, Zhu RL. 2016. World checklist of hornworts and liverworts. PhytoKeys. 59:1–828.
- Stephani F. 1899. Species hepaticarum. Fimbriaria. Bull. Herb. Boissier. 7:84–110; 198–225.

## Supplemental material

314 **Supplementary Table 1.** Analysed samples of *Exormotheca* species with the description of the  
315 geographic location, voucher information, and sampling code.

Taxon	Geographic location	Voucher no. (Herbarium)	Sampling code
<i>Exormotheca pustulosa</i> Mitt.	Portugal, Madeira	266739 (LISU)	EXPMD10
<i>Exormotheca pustulosa</i>	Portugal, Madeira	266734 (LISU)	EXPMD4
<i>Exormotheca pustulosa</i>	Portugal, Madeira	266735 (LISU)	EXPMD4.1
<i>Exormotheca pustulosa</i>	Portugal, Madeira	266736 (LISU)	EXPMD4.2
<i>Exormotheca pustulosa</i>	Portugal, Madeira	266737 (LISU)	EXPMD4.3
<i>Exormotheca pustulosa</i>	Portugal, Porto Santo	261316 (LISU)	EXP_L261316
<i>Exormotheca pustulosa</i>	Portugal, Algarve	266740 (LISU)	EXPA1
<i>Exormotheca pustulosa</i>	Portugal, Algarve	266741 (LISU)	EXPA2
<i>Exormotheca pustulosa</i>	Portugal, Algarve	266742 (LISU)	EXPA3
<i>Exormotheca pustulosa</i>	Portugal, Algarve	266743 (LISU)	EXPA8
<i>Exormotheca pustulosa</i>	Portugal, Azores, Faial	266744 (LISU)	EXPF21
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, La Palma	25169 (Dirkse)	EXP_LP1
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, La Palma	25172 (Dirkse)	EXP_LP2
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, La Gomera	33156 (Dirkse)	EXP_LG1
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, La Gomera	32448 (Dirkse)	EXP_LG2
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, Hierro	30398 (Dirkse)	EXP_HIE1
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, Tenerife	26622 (Dirkse)	EXP_TE1
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, Tenerife	26612 (Dirkse)	EXP_TE2
<i>Exormotheca pustulosa</i>	Spain, Canary Islands, Gran Canaria	27618 (Dirkse)	EXP_GCN1
<i>Exormotheca pustulosa</i>	South Africa	0760429-0 (PRE)	EXPSAF1
<i>Exormotheca pustulosa</i>	South Africa	0790964-0 (PRE)	EXPSAF2
<i>Exormotheca pustulosa</i>	South Africa	0790869-0 (PRE)	EXPSAF3
<i>Exormotheca pustulosa</i>	South Africa	0570538-0 (PRE)	EXPSAF4
<i>Exormotheca pustulosa</i>	South Africa	0580243-0 (PRE)	EXPSAF5
<i>Exormotheca pustulosa</i>	South Africa	0580241-0 (PRE)	EXPSAF6
<i>Exormotheca pustulosa</i>	South Africa	0580247-0 (PRE)	EXPSAF7
<i>Exormotheca pustulosa</i>	South Africa	0581355-0(PRE)	EXPSAF8
<i>Exormotheca pustulosa</i>	South Africa	0570539-0(PRE)	EXPSAF9
<i>Exormotheca pustulosa</i>	South Africa	0564790-0 (PRE)	PRE564790
<i>Exormotheca pustulosa</i>	Reunion Island	0992184-0 (PRE)	EXPPRE1
<i>Exormotheca pustulosa</i>	Kenya	0992181-0 (PRE)	EXPKY2
<i>Exormotheca pustulosa</i>	Tanzania	00884125 (E)	EXP_TZ1
<i>Exormotheca pustulosa</i>	Saint Helena	00884120 (E)	EXP_SH1
<i>Exormotheca pustulosa</i>	Saint Helena	00884121 (E)	EXP_SH2
<i>Exormotheca pustulosa</i>	Saint Helena	00884122 (E)	EXP_SH3
<i>Exormotheca pustulosa</i>	Saint Helena	00884123 (E)	EXP_SH4
<i>Exormotheca pustulosa</i>	Oman	00884118 (E)	EXPOM1
<i>Exormotheca martins-loussaoae</i> Sim-Sim, A.Martins, J.Patiño & C.A.Garcia	Cape Verde, Santo Antão	266748 (LISU)	EXPSA5
<i>Exormotheca martins-loussaoae</i>	Cape Verde, Santo Antão	266745 (LISU)	EXPSA2
<i>Exormotheca martins-loussaoae</i>	Cape Verde, Santo Antão	266746 (LISU)	EXPSA2.1
<i>Exormotheca martins-loussaoae</i>	Cape Verde, Santo Antão	266747 (LISU)	EXPSA2.2
<i>Exormotheca martins-loussaoae</i>	Cape Verde, Santo Antão	(LISU)	EXPSA16

<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266749 (LISU)	EXPSN08.1
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266750 (LISU)	EXPSN08.2
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266751 (LISU)	EXPSN08.3
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266752 (LISU)	EXPSN08.4
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266753 (LISU)	EXPSN10
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266754 (LISU)	EXPSN011
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266755 (LISU)	EXPSN012
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266756 (LISU)	EXPSN16
<i>Exormotheca martins-loussaoae</i>	Cape Verde, São Nicolau	266757 (LISU)	EXPSN18
<i>Exormotheca martins-loussaoae</i>	Cape Verde, Fogo	266758 (LISU)	EXPFG1
<i>Exormotheca martins-loussaoae</i>	Cape Verde, Fogo	266759 (LISU)	EXPFG2
<i>Exormotheca welwitschii</i> Steph.	Portugal, Algarve	264421 (LISU)	EXWPTF1
<i>Exormotheca welwitschii</i>	Portugal, Algarve	266762 (LISU)	EXW_A1
<i>Exormotheca welwitschii</i>	Portugal, Estremadura	264421 (LISU)	EXWL264421
<i>Exormotheca holstii</i> Steph.	South Africa	266763 (LISU)	EXHOL1
<i>Exormotheca holstii</i>	South Africa	266764 (LISU)	EXHOL3
<i>Exormotheca holstii</i>	South Africa	0891437-0 (PRE)	EXHOL4
<i>Exormotheca holstii</i>	South Africa	0758805-0 (PRE)	EXHOL2R

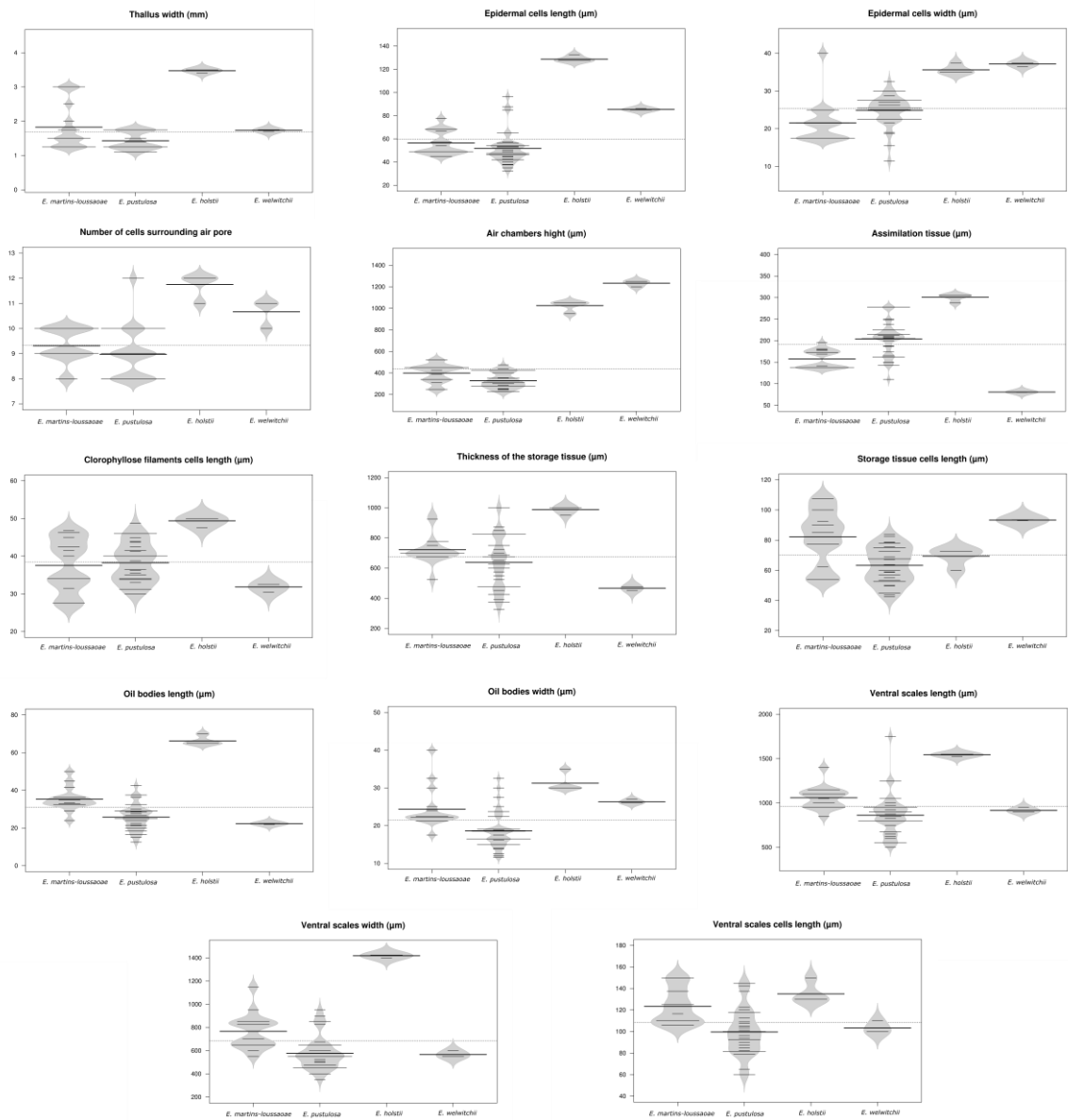
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**Supplementary Figure 1.** Beanplots of the most informative gametophyte quantitative and significant variables of *Exormotheca* studied species. The long line on each bean is the mean of all observations, the shape of the bean is a mirrored density curve, and the short black bars represent each data point. The dotted horizontal line across the plot is set to overall mean.

335 **Table 1.** Results of significant quantitative and qualitative characters to distinguish the *Exormotheca* studied species. ANOVA F statistic and significance  
336 level (\*\*\*)  $p < 0.001$ ) for each variable and four species is given. Letters (a,b,c) represent the different groups resulted from a post-hoc Tukey test for  
337 statistically significant variables.

	<i>Exormotheca martins-loussaoae</i> (n=16)		<i>Exormotheca pustulosa</i> (n=37)		<i>Exormotheca holstii</i> (n=4)		<i>Exormotheca welwitchii</i> (n=3)		ANOVA
	Mean $\pm$ SD	Min–Max	Mean $\pm$ SD	Min–Max	Mean $\pm$ SD	Min–Max	Mean $\pm$ SD	Min–Max	
<b>Quantitative characters</b>									
<b>Thallus width (mm)</b>	1.8 $\pm$ 0.7 (b)	1.25–3	1.4 $\pm$ 0.3 (a)	1.1–1.75	3.5 $\pm$ 0.0.1 (c)	3.4–3.5	1.7 $\pm$ 0.01 (ab)	1.7–1.75	31.18***
<b>Air chambers rows</b>	7.2 $\pm$ 0.75 (a)	6–9	8.9 $\pm$ 0.5 (a)	8–10	14.25 $\pm$ 0.5 (c)	14–15	11.3 $\pm$ 0.6 (b)	11–12	51.01***
<b>Epidermal cells length (<math>\mu</math>m)</b>	56.1 $\pm$ 10.7 (a)	45.0–77.5	51.7 $\pm$ 13.6 (a)	32.5–96.5	128.8 $\pm$ 2.5 (c)	127.5–132.5	85.3 $\pm$ 0.6 (b)	85–86	53.09***
<b>Epidermal cells width (<math>\mu</math>m)</b>	21.6 $\pm$ 5.7 (a)	17.5–40	24.8 $\pm$ 4.1 (a)	11.5–32.5	35.6 $\pm$ 1.3 (b)	35–37.5	37.2 $\pm$ 0.6 (b)	36.5–37.5	18.42***
<b>Number of cells surrounding air pore</b>	9.3 $\pm$ 0.7 (a)	8–10	9 $\pm$ 1 (b)	8–12	11.75 $\pm$ 0.5 (c)	11–12	10.6 $\pm$ 0.6 (c)	10–11	30.24***
<b>Air chambers high (<math>\mu</math>m)</b>	398.9 $\pm$ 85.4 (b)	247.5–520	327.7 $\pm$ 70.3 (a)	225–475	1025 $\pm$ 50 (c)	950–1050	1233 $\pm$ 28.9 (d)	1200 - 1250	235.80***
<b>Assimilation tissue (<math>\mu</math>m)</b>	157.7 $\pm$ 21.1 (b)	137.5–195	204 $\pm$ 40.5 (c)	110–277.5	300.6 $\pm$ 8.8 (d)	287.5–305	80.7 $\pm$ 0.6 (a)	80–81	30.63***
<b>Number of cells in clorophyllose filaments</b>	5.5 $\pm$ 0.5 (b)	5–6	6.8 $\pm$ 1.3 (c)	5–9	7.75 $\pm$ 0.5 (c)	7–8	3 $\pm$ 0 (a)	3–3	15.49***
<b>Clorophyllose filaments cells length (<math>\mu</math>m)</b>	37.5 $\pm$ 7.1 (a)	27.5–46.8	38.2 $\pm$ 5.2 (a)	30–48.8	49.4 $\pm$ 1.3 (b)	47.5–50	31.8 $\pm$ 1.20 (a)	30.5–32.5	6.65***
<b>Thickness of the storage tissue (<math>\mu</math>m)</b>	721.9 $\pm$ 98.7 (b)	525–950	637.4 $\pm$ 178 (ab)	325–1000	987.5 $\pm$ 25 (c)	950–1000	466.7 $\pm$ 14.4 (a)	450–475	8.81***
<b>Storage tissue cells length (<math>\mu</math>m)</b>	82.2 $\pm$ 18.2 (b)	54–107.5	63.3 $\pm$ 11.9 (a)	42.5–83.8	69.4 $\pm$ 6.3 (ab)	60–72.5	93.3 $\pm$ 0.3(b)	93–93.5	10.32***
<b>Oil bodies length (<math>\mu</math>m)</b>	35.4 $\pm$ 6 (b)	24–50	25.8 $\pm$ 6.8 (a)	12.5–42.5	66.3 $\pm$ 2.5 (c)	65–70	22.3 $\pm$ 0.3 (a)	22.0 - 22.5	54.40***
<b>Oil bodies width (<math>\mu</math>m)</b>	24.2 $\pm$ 5.5 (b)	17.5–40	18.6 $\pm$ 4.8 (a)	11.7–32.5	31.3 $\pm$ 2.5 (b)	30–35	26.3 $\pm$ 0.6 (b)	26–27	12.5***
<b>Ventral scales length (<math>\mu</math>m)</b>	1059.4 $\pm$ 128.1 (b)	850–1400	862.8 $\pm$ 232.2 (a)	500–1750	1543.8 $\pm$ 12.5 (c)	1525–1550	916.7 $\pm$ 28.9 (ab)	900–950	15.99***
<b>Ventral scales width (<math>\mu</math>m)</b>	767.2 $\pm$ 152.7 (a)	550–1150	577.2 $\pm$ 142.5 (b)	350–950	1419.0 $\pm$ 12.5 (c)	1400–1425	566 $\pm$ 28.9 (ab)	550–600	47.13***
<b>Ventral scales cells length (<math>\mu</math>m)</b>	123.4 $\pm$ 16.7 (b)	106–150	99.6 $\pm$ 21.8 (a)	60–145	135 $\pm$ 10 (b)	130–150	103.3 $\pm$ 5.8 (ab)	100–110	8.07***
<b>Qualitative characters</b>									
<b>Ventral scales (color)</b>	dark purple more than 1/2		purple or partly hyaline		purple from base to 1/2		hyaline		–
<b>Air Chambers (shape)</b>	Conical		pustular or conical		conical		pustular		–
<b>Thallus (color)</b>	dark green		glaucous green or silvery green		glaucous		glaucous		–

339 **Figure captions**

340

341 **Figure 1.** *Exormotheca martins-loussaoae*. (A) Hydrated thallus with rows of antheridia in grooves  
342 and with young gynoecium, (B) Hydrated thallus with young and mature carpocephalum and 2  
343 capsules exerted laterally, (C) Dry thallus covered by dark scales, (D) Dry thallus with mature  
344 carpocephalum, (E) Thallus with numerous prominent conical evaginations, (F) Air pores.

345

346 **Figure 2.** *Exormotheca martins-loussaoae*. (A) Thallus section from apex to base, (B) Air chamber  
347 with chlorophyllose filaments, (C) Scale, (D) Cells of the storage tissue with oil bodies, (E) Ultraviolet  
348 picture of air chamber under 330-385 nm.

349

350 **Figure 3.** SEM of spores. (A–C) *Exormotheca martins-loussaoae* (holotype, LISU 266756), and (D–  
351 F) *Exormotheca pustulosa* (LISU 266739), (A, D) Distal face, (B) Distal and proximal face, (C–F)  
352 Papillae opening, (E) Proximal face.

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354 **Figure 4.** Known distribution of *Exormotheca martins-loussaoae*.

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