

cryptogamie

Bryologie

2022 • 43 • 13

Observations on the taxonomy and distribution
of *Eipterygium atlanticum* Hanusch
and *E. tozeri* (Grev.) Lindb. (Mniaceae Schwägr.)
in mainland Portugal

Cecília SÉRGIO, César A. GARCIA &
Ron D. PORLEY



DIRECTEUR DE LA PUBLICATION / *PUBLICATION DIRECTOR*: Bruno David
Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / *EDITOR-IN-CHIEF*: Denis LAMY

ASSISTANTE DE RÉDACTION / *ASSISTANT EDITOR*: Chris LE COQUET-LE ROUX (bryo@cryptogamie.com)

MISE EN PAGE / *PAGE LAYOUT*: Chris LE COQUET-LE ROUX

RÉDACTEURS ASSOCIÉS / *ASSOCIATE EDITORS*

Biologie moléculaire et phylogénie / *Molecular biology and phylogeny*

Bernard GOFFINET

Department of Ecology and Evolutionary Biology, University of Connecticut (United States)

Mousses d'Europe / *European mosses*

Isabel DRAPER

Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid (Spain)

Francisco LARA GARCÍA

Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid (Spain)

Mousses d'Afrique et d'Antarctique / *African and Antarctic mosses*

Rysiek OCHYRA

Laboratory of Bryology, Institute of Botany, Polish Academy of Sciences, Krakow (Pologne)

Bryophytes d'Asie / *Asian bryophytes*

Rui-Liang ZHU

School of Life Science, East China Normal University, Shanghai (China)

Bioindication / *Biomonitoring*

Franck-Olivier DENAYER

Faculté des Sciences Pharmaceutiques et Biologiques de Lille, Laboratoire de Botanique et de Cryptogamie, Lille (France)

Écologie des bryophytes / *Ecology of bryophyte*

Nagore GARCÍA MEDINA

Department of Biology (Botany), and Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid (Spain)

COUVERTURE / *COVER*:

Extraits d'éléments de la Figure 1 / Extracts of the Figure 1

Cryptogamie, Bryologie est indexé dans / *Cryptogamie, Bryologie is indexed in*:

- Biological Abstracts
- Current Contents
- Science Citation Index
- Publications bibliographiques du CNRS (Pascal).

Cryptogamie, Bryologie est distribué en version électronique par / *Cryptogamie, Bryologie is distributed electronically by*:

- BioOne® (<http://www.bioone.org>)

Cryptogamie, Bryologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Bryologie is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish: Adansonia, Geodiversitas, Zoosystema, Anthropolozologica, European Journal of Taxonomy, Naturae, Comptes Rendus Palevol, Cryptogamie sous-sections Algologie, Mycologie.*

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <http://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2022

ISSN (imprimé / *print*) : 1290-0796 / ISSN (électronique / *electronic*) : 1776-0992

Observations on the taxonomy and distribution of *Epipterygium atlanticum* Hanusch and *E. tozeri* (Grev.) Lindb. (Mniaceae Schwägr.) in mainland Portugal

Cecília SÉRGIO
César A. GARCIA

Universidade de Lisboa, Museu Nacional de História Natural e da Ciência,
CE3C-Centre for Ecology, Evolution and Environmental Changes,
Rua da Escola Politécnica, 58, 1250-102 Lisboa (Portugal)
and Universidade de Lisboa, Faculdade de Ciências, Departamento de Biologia Vegetal,
CE3C-Centre for Ecology, Evolution and Environmental Changes, Lisboa (Portugal)
csergio@fc.ul.pt (corresponding author)

Ron D. PORLEY
Cerca dos Pomares, 8670-052 Aljezur (Portugal)

Submitted on 30 October 2021 | Accepted on 9 June 2022 | Published on 9 November 2022

Sérgio C., Garcia C. A. & Porley R. D. 2022. — Observations on the taxonomy and distribution of *Epipterygium atlanticum* Hanusch and *E. tozeri* (Grev.) Lindb. (Mniaceae Schwägr.) in mainland Portugal. *Cryptogamie, Bryologie* 43 (13): 195-200. <https://doi.org/10.5252/cryptogamie-bryologie2022v43a13>. <http://cryptogamie.com/bryologie/43/13>

ABSTRACT

Epipterygium atlanticum Hanusch is a recently described species based on plants occurring mainly in Macaronesia, with one collection from Scotland. Against this background, we studied 144 specimens of *E. tozeri* s.l. in LISU herbarium from mainland Portugal, including recent field collections, and 70 were referable to *E. atlanticum*. The length and width of mid-leaf laminal cells of lateral leaves were the most important morphological characters for the delimitation of the two European species. *Epipterygium atlanticum* is a widely distributed taxon throughout the Portuguese territory, becoming more frequent in Atlantic zones and in the Algarve. We provide an updated map of the distribution of both species and a brief account of their ecology and habitat preferences.

KEY WORDS

Europe,
Portugal,
Mniaceae,
morphology,
ecology,
distribution.

RÉSUMÉ

Observations sur la taxonomie et la distribution de Epipterygium atlanticum Hanusch et E. tozeri (Grev.) Lindb. (Mniaceae Schwägr.) au Portugal continental.

Epipterygium atlanticum Hanusch est une espèce récemment décrite principalement présente en Macaronésie, avec une collection en Écosse. Dans ce contexte, nous avons étudié 144 spécimens de *E. tozeri* s.l. du Portugal continental conservés dans l'herbier LISU, incluant des récoltes récentes, et 70 étaient attribuables à *E. atlanticum*. La longueur et la largeur des cellules laminales des feuilles latérales s'avèrent être les caractères morphologiques les plus importants pour la délimitation de deux espèces. *Epipterygium atlanticum* est un taxon largement répandu sur tout le territoire portugais, devenant de plus en plus fréquent dans les zones atlantiques et en Algarve. Nous fournissons une carte sur la distribution des deux espèces ainsi qu'un bref compte-rendu sur leur écologie et leurs préférences en matière d'habitat.

MOTS CLÉS

Europe,
Portugal,
Mniaceae,
morphologie,
écologie,
distribution.

INTRODUCTION

The largely tropical genus *Epipterygium* Lindb. (Mniaceae), conceived by Lindberg in 1862 to initially accommodate two taxa, *E. wrightii* (Sull.) Lindb. and *E. jamaicense* Lindb., currently comprises 17 validly described species but has not been revised worldwide since Brotherus (1925). *Epipterygium* in Europe is distinguished by its dimorphic leaves, larger lateral leaves and smaller dorsal leaves, arranged in one or two rows on the stem. Sometimes these character states are weakly expressed, particularly towards the apex of a stem or on fertile stems and they can be difficult to observe. The genus includes *Epipterygium tozeri* (Grev.) Lindb. (described in 1827 as *Bryum tozeri* Grev.), the only member of the genus that extends into temperate regions with an intercontinental disjunct range (Ochi 1955; Shaw 1984; Arts & Nordhorn-Richter 1986), prompting Hanusch *et al.* (2020) to hypothesize that these widely disjunct populations represent distinct taxonomic entities. Their phylogenetic analysis revealed that the *E. tozeri* complex consists of four previously overlooked genetically and morphologically distinct taxa including *E. atlanticum* Hanusch, a species occurring mainly in Macaronesia (Azores, Madeira & Canary Islands) with one collection from Europe (Scotland). *Epipterygium tozeri* s.s. was shown to be largely confined to Europe (with one collection from Madeira). However, relatively few specimens from mainland Portugal were sequenced in the phylogenetic analysis of Hanusch *et al.* (2020); only seven collections were included from a total of 76 collections of *Epipterygium* from all regions (62 from Europe), and only two were from LISU.

Against this background, we looked at all collections (130 specimens) of *Epipterygium* in LISU herbarium and also some recent collections (14 specimens) from the Algarve, mostly from Serra de Monchique collected by R. D. Porley, using the same morphometric characters described in Hanusch *et al.* (2020). Shaw (1984) employed similar continuous characters in his taxonomic study of *Epipterygium* of North America and highlighted the importance of precisely defining where measurements are made regarding stem length and cell dimensions of lateral leaves. There is considerable variation in cell dimensions on the same leaf towards the costa or margin, or proximally (near the base) or distally (near apex) in lateral leaves.

The present study aims to clarify the occurrence and distribution of the newly described *Epipterygium atlanticum* and *E. tozeri* in mainland Portugal.

MATERIAL AND METHODS

SAMPLING DESIGN AND CHARACTER MEASUREMENTS

Following the methodology of Hanusch *et al.* (2020), we made an initial assessment of the morphological variability within all mainland Portuguese specimens labelled as *Epipterygium tozeri* in LISU, based on measurements of ten continuous characters plus ratios, including habit, plant size, median cell length and width, and costa length of five to ten mature well-developed lateral leaves (excluding perichaetial or perigonal

leaves or from etiolated stems). We selected a homogenous mid-leaf area (Fig. 1) with *c.* 30–50 cells and measured the length and width of ten cells per leaf.

We paid particular attention to material of *E. tozeri* s.l. from Pico (Azores) in LISU, as it was reasonable to assume that it represented *E. atlanticum*, given that all Azorean material sequenced by Hanusch *et al.* (2020) nested within their ‘Macaronesian clade’, thus enabling us to become conversant with the differences between the new species and *E. tozeri*. In the early stages of our study it soon became apparent that some characters showed significant variation and overlap and so we focused on a reduced subset of characters, the most important of which was median cell length. Not all character state measurements (such as dorsal leaf length, costa length, marginal cell dimensions which all show large variation) employed by Hanusch *et al.* (2020) were included in this work; only those initially judged to be important in distinguishing the two taxa, including plant size (i.e., stem length), median cell length, width and ratio from lateral leaves were considered (Fig. 2).

We studied 144 collections but made only 125 measurements from selected specimens representing all provinces in mainland Portugal (Sérgio & Carvalho 2003). Following the revision of the selected herbarium specimens, combined with the geo-referenced localities, we prepared a database for the two species, *Epipterygium tozeri* and *E. atlanticum*, where information was available from adequately labelled vouchers, the altitudinal range and ecological preferences noted.

RESULTS

Family MNIACEAE Schwägr.

Genus *Epipterygium* Lindb.

Epipterygium tozeri (Grev.) Lindb. s.s.

SELECTED SPECIMENS EXAMINED. — **Portugal.** Minho, Celorico de Basto, Canedo de Basto, Parque de lazer, 41°26'48"N, 7°57'52"W, 138 m a.s.l., 26.XI.2010, leg. C. Sérgio, C. Garcia (LISU[LISU 239535]); Beira Alta, Gouveia, Ribamondego, 40°34'16"N, 7°35'12"W, 282 m a.s.l., 12.IV.2011, leg. C. Sérgio, C. Garcia, (LISU[LISU 244744]); Algarve, Ribeira de Seixe, 37°24'19"N, 8°43'04"W, 500 m a.s.l., 22.II.2016, leg. Porley (Herb. Porley).

Epipterygium atlanticum Hanusch

SELECTED SPECIMENS EXAMINED. — **Portugal.** Trás-os-Montes e Alto Douro, Bragança, Rebordelo, Rio Rabaçal, 41°27'26"N, 7°32'04"W, 415 m a.s.l., 01.VII.2011, leg. F. Aguiar, F. Reis (LISU[LISU 246865]); Baixo Alentejo, Odemira, próximo da Ribeira de Vale de Gomes, cruzamento para a Zambujeira, 37°34'40"N, 8°42'27"W, 20 m a.s.l., 04.II.2002, leg. C. Garcia (LISU[LISU 204992]); Algarve, Monchique, road to Picota summit, Serra de Monchique, 37°18'29"N, 8°31'54"W, 482 m a.s.l., 08.III.2017, leg. Porley (Herb. Porley).

TAXONOMIC CONCLUSIONS

The results of our measurements of continuous characters are presented in the same sequence as given in appendix 1 of

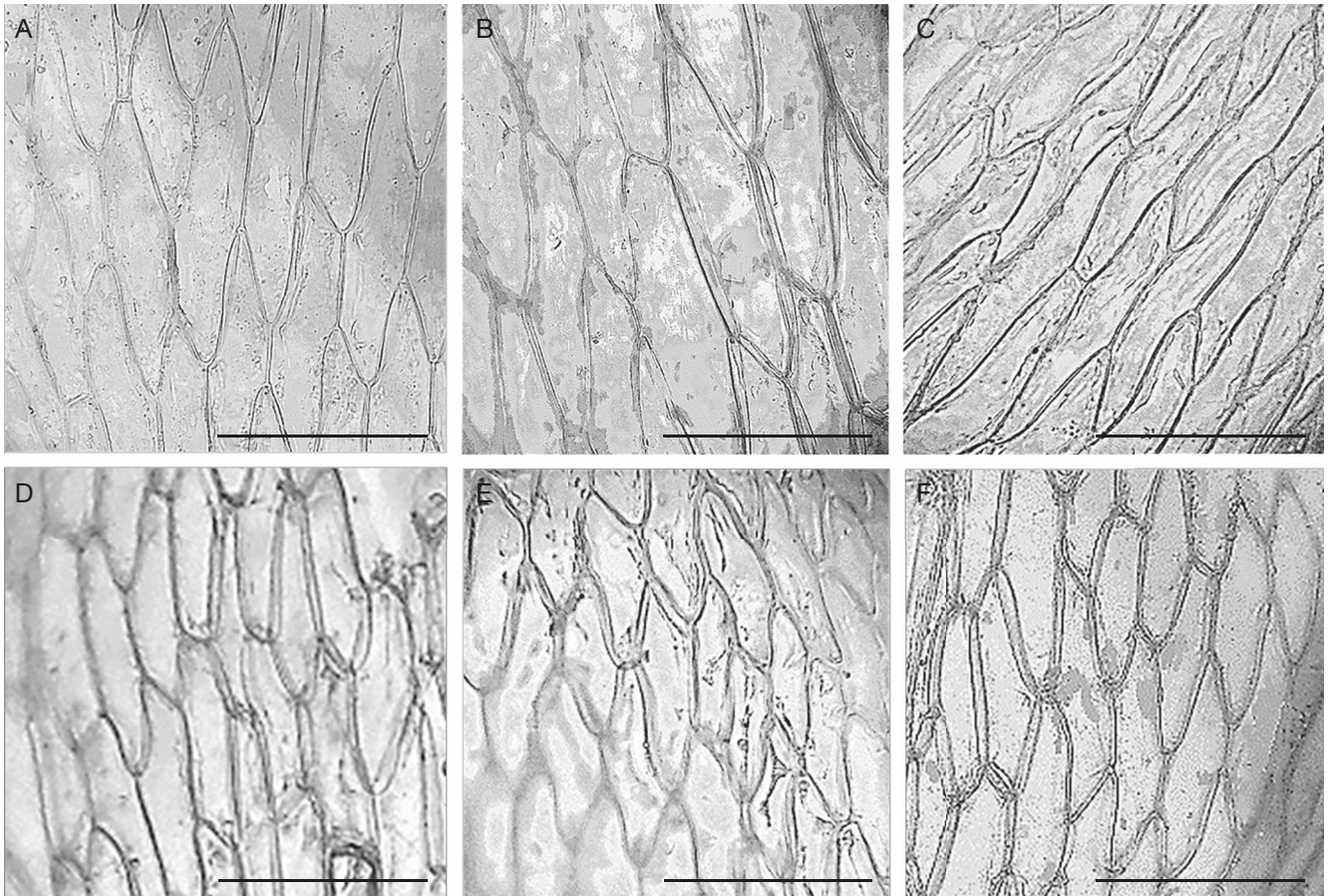


FIG. 1. — Areolation in mid-leaf, lateral leaves: **A-C**, *Epipterygium tozeri* s.s.; **A**, Celorico de Bastos, LISU[LISU 239535]; **B**, Gouveia, Ribamondego, LISU[LISU 244744]; **C**, Ribeira de Seixe, Herb. Porley; **D-F**, *Epipterygium atlanticum* Hanusch; **D**, Monchique, Picota summit, Herb. Porley; **E**, Rabaçal, LISU[LISU 246865]; **F**, Odemira, LISU[LISU 204992]. Scale bars: 100 μ m.

Hanusch *et al.* (2020). We considered median cell length to have the greatest taxonomic value. The results of the analyses are presented in Figure 2.

From the selected collections indicated as *Epipterygium tozeri* s.l., we found 70 corresponded to *Epipterygium atlanticum* and 55 to *Epipterygium tozeri* s.s. (Fig. 2). Measurements for most of the characters obtained from the Portuguese material were generally of lesser dimensions than given in Hanusch *et al.* (2020), but the overall differentiation between the two taxa was still maintained. Specimens of *E. atlanticum* and *E. tozeri* s.s. were most clearly separated by measuring the mid-leaf cell length of the lateral leaves. In Portuguese *E. atlanticum* the cell length is 85–130 μ m, while Hanusch *et al.* (2020) gives the mean value mid-leaf cell length as 109.5 μ m for the ‘Macaronesian’ clade (i.e., *E. atlanticum*). In Portuguese *E. tozeri* s.s. the cell length is 124–185 μ m, with a mean value of 156.6 μ m. Hanusch *et al.* (2020) gives a minimum cell length of 139 μ m, with a mean of 170 μ m. Values of the mean of the median cell length: width ratio indicates that the cells in *E. atlanticum* are consistently less elongated and occasionally hexagonal-rectangular and with slightly undulate walls. Length: width ratio values for *E. atlanticum* are less than 4.4 while for *E. tozeri* s.s. they are mostly up to 5.6–(7.0), they are thus much longer than wide with

a tendency to have straight walls, in contrast to the slightly undulate walls of *E. atlanticum*.

An additional feature, not mentioned in Hanusch *et al.* (2020), is the laminal areolation. Whilst the cells are approximately the same width in both species, in *E. atlanticum* they are shorter with less straight longitudinal walls giving a somewhat sigmoidal shape to the mid-laminal cells (Fig. 1).

ECOLOGY AND DISTRIBUTION

The two species of *Epipterygium* overlap in their ecological preferences and are both associated with a wide range of companion bryophytes. *Epipterygium atlanticum* and *E. tozeri* occur on tracks and paths in at least partially shaded niches, and on shady, rocky slopes, on acidic soils or other substrates between rocks. *Epipterygium tozeri* appears to be more tolerant of competition, while *E. atlanticum* appears to be less tolerant of close competition and is often present in sites that are subject to periodic desiccation and on bare soil of tracks and paths in wooded habitats, including shady *Rhododendron* ravines. However, both species can coexist in the same area, though *E. tozeri* s.s. is found mainly in mixed species populations, rarely as pure tufts. *Epipterygium atlanticum* also occurs in localities supporting bryophytes of phytogeographic interest with disjunct distributions such as

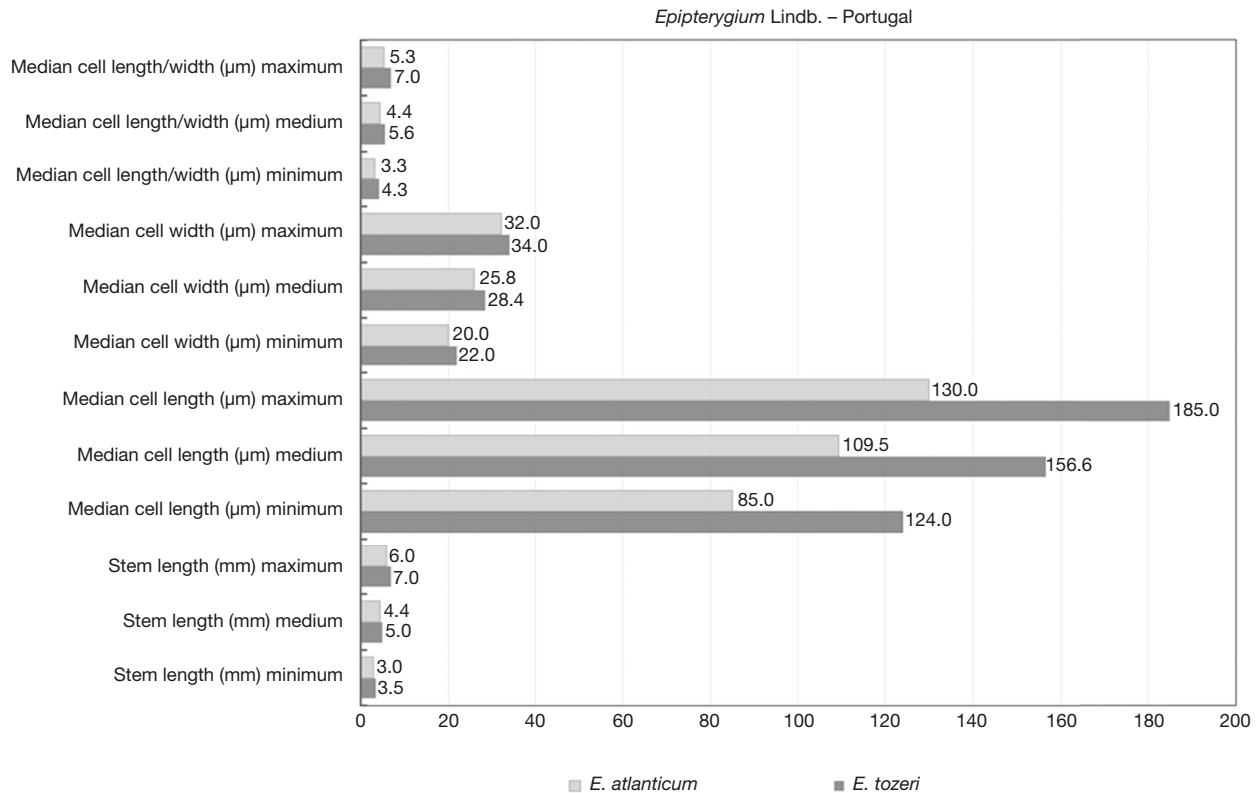


FIG. 2. — Quantitative characters and measurements (mean values in µm) of the 125 Portuguese studied samples of *Epipterygium atlanticum* Hanusch and *E. tozeri* s.s.

Bryoerythrophyllum campylocarpum (Müll.Hal.) H.A.Crum, *Campylostelium strictum* Solms., *Fissidens curvatus* Hornsch. and *Ptychostomum minii* (Podp. ex Guim.) D.Bell & Holyoak. It is notable that among the bryophytes that can cohabit with *E. tozeri* s.l. is *Claopodium whippleanum* (Sull.) Renauld & Cardot, a moss reported by Shaw (1984) as a species associated with *E. tozeri* in California. Approximately 15% of the Portuguese localities with *Epipterygium tozeri* s.l. are known to support *C. whippleanum*.

Epipterygium tozeri s.l. presents a disjunct distribution globally, and Arts & Nordhorn-Richter (1986) have suggested it is a Tertiary relict, from a southern coastal Laurasian origin. It is a Mediterranean-Atlantic species, known in Europe, Asia, North Africa, and North-West America (Shaw 1984). In Europe it is most widespread in the south-west, from the Mediterranean region north to the British Isles, and is less common in the eastern part of the continent (Campisi & Cogoni 2019; Hodgetts & Lockhart 2020). Within the Iberian Peninsula *Epipterygium tozeri* s.l. is particularly frequent around the Mediterranean margin from the Algarve to Barcelona (Brugués *et al.* 2021), less so on the Central Meseta, and it also occurs further north on the peninsula, but is apparently limited by altitude (Cano 2010).

The distribution of *Epipterygium atlanticum* and *E. tozeri* s.s. in Portugal is presented in Figure 3A. *Epipterygium atlanticum* has a scattered distribution across the entire country with an elevational range in Portugal to 855 m (Fig. 3B); *Epipterygium tozeri* s.s. however shows a tendency to extend to higher alti-

tudes. It is likely that *E. atlanticum* is a widespread species in xerophilous vegetation in other Mediterranean-Atlantic climatic regions of Europe and Macaronesia.

DISCUSSION

Overall, we found close agreement with Hanusch *et al.* (2020) for the newly recognised lineages of *Epipterygium atlanticum* and *E. tozeri* s.s. using mid-leaf median cell length from a series of lateral leaves. However, the use of stem size as a defining continuous character was problematic during the present study. Hanusch *et al.* (2020) states *E. tozeri* s.l. from Macaronesian origin never exceeds 4 mm in size (however, in the key the dichotomy states “gametophyte up to 5 mm long”) whereas *E. tozeri* grows up to 13 mm tall (in the key “gametophyte more than 5 mm long”).

Although we considered the size of the plant in our study, we soon had reservations regarding its potential to safely discriminate the species, particularly given that *Epipterygium* is a small orthotropic plant. Size, or stem length, is a measure of a plant’s structural architecture, or growth-form. The height of a plant can be influenced by the environment, particularly the availability of light and water (Mägdefrau 1982). *Epipterygium* is characterized by a turf or scattered turf life-form (Hill *et al.* 2007) indicative of low moisture regimes (Gimingham & Birse 1957), and thus growth-form and life-form are clearly linked. A further issue is that Hanusch *et al.* (2020) empha-

sizes that *Epipterygium atlanticum* is complanate, and uses this character in the key; however, this trait is not mentioned in the generic description preceding the key, neither is it given in the description of *E. atlanticum*. It should be noted that very few of the inferred *E. atlanticum* examined during our present study demonstrated a complanate habit; most plants show spreading leaves that are more or less spirally arranged around the stem. The literature is also inconsistent when applying the term complanate to *E. tozeri* s.l. (Smith 2004; Cortini Pedrotti 2006; Frey *et al.* 2006). Casas *et al.* 2020 do not mention the complanate habit, whereas Cano (2010) describes leaves as “frequently complanate” in the generic description, yet “more or less complanate” in the description of *E. tozeri* s.l., thus suggesting inherent variation, rather than implicitly recognizing a cryptic taxon.

The present study suggests that *E. atlanticum* is likely to be a more widespread species in Mediterranean-Atlantic climate areas of Europe, and also in Macaronesia, though rarely or never in the arctic-alpine region. Finally, despite comprising only two known species in Europe, *Epipterygium* is a somewhat challenging genus for taxonomists due to the lack of invariable characters and the possible presence of transitional morphotypes. Sporophytes appear to be fairly frequent in material in LISU from mainland Portugal and may provide an opportunity for further studies on the differences between this pair of species.

Acknowledgements

The research was co-funded by the Portuguese National Funds, through FCT “Fundação para a Ciência e a Tecnologia”, within the thematic line TL1 – Integrated ecological assessment of environmental change on biodiversity of the project UIDB/00329/2020. The authors wish to express their gratitude to all the reviewers and to the editors for their valuable suggestions.

REFERENCES

- ARTS T. & NORDHORN-RICHTER G. 1986. — *Epipterygium tozeri* in Europe, its distribution and vegetative propagation. *Journal of Bryology* 14: 91-97. <https://doi.org/10.1179/jbr.1986.14.1.91>
- BROTHERUS V. F. 1925. — Musci (Laubmoose), in ENGLER H. G. A. & PRANTL K. (eds), *Nat. Pflanzenfam* 11. Duncker & Humblot, Berlin: 542, fig. 796.
- BRUGUÉS M., CROS R. M. & SÉRGIO C. 2021. — *Epipterygium tozeri* (Grev.) Lindb. Barcelona. Available from <http://briofits.iec.cat>. (accessed on 2 May 2021).
- CAMPISI P. & COGONI A. 2019. — *Epipterygium tozeri*. *The IUCN Red List of Threatened Species 2019*: e.T84259912A87771452.
- CANO M. J. 2010. — *Epipterygium* Lindb., in GUERRA J., CANO M. J. & ROS R. (eds), *Flora Briofítica Ibérica IV*. Universidad de Murcia-Sociedad Española de Briología, Murcia, 317 p.
- CASAS C., BRUGUÉS M., CROS R. M., SÉRGIO C. & INFANTE M. 2020. — *Handbook of Mosses of the Iberian Peninsula and the Balearic Islands. Illustrated Keys to genera and species*. Institut d'Estudis Catalans, Barcelona, 379 p.
- CORTINI PEDROTTI C. 2006. — *Flora dei Muschi d'Italia*. Bryopsida (II parte). A. Delfino editore, Roma, 416 p.

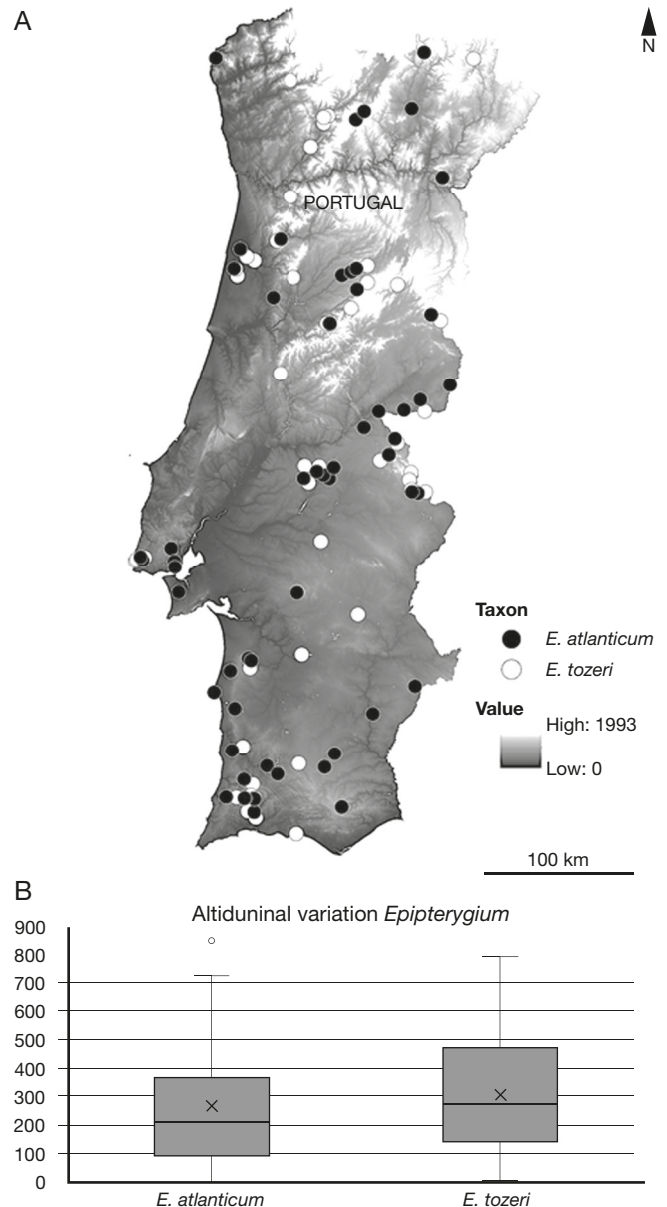


FIG. 3. — **A**, distribution of *Epipterygium atlanticum* Hanusch and *E. tozeri* s.s. in mainland Portugal based on revised LISU and samples from Algarve (Herb. Porley). Intensity of shading corresponds to altitudinal data (0 to 1993); **B**, box plots showing the variation (0 to 900 m) in locality elevation for the two taxa.

- FREY W., FRAHM J.-P., FISCHER E. & LOBIN W. 2006. — *The Liverworts, Mosses and Ferns of Europe*. Harley Books, Colchester, 512 p.
- GIMINGHAM C. H. & BIRSE E. M. 1957. — Ecological studies on growth-form in bryophytes. I. Correlations between growth-form and habitat. *Journal of Ecology* 45: 533-545.
- GREVILLE R. K. 1827. — *Scottish Cryptogamic Flora*. Vol. 5. Maclachlan & Stewart, Edinburgh; Craddock & Joy, Baldwin, pls 271-300.
- HANUSCH M., ORTIZ E. M., PATINO J. & SCHAEFER H. 2020. — Biogeography and integrative taxonomy of *Epipterygium* (Mniaceae, Bryophyta). *Taxon* 69 (6): 1150-1171. <https://doi.org/10.1002/tax.12324>
- HILL M. O., PRESTON C. D., BOSANQUET S. D. S. & ROY D. B. 2007. — *Bryoatt: Attributes of British and Irish Mosses, Liverworts and Hornworts*. Centre for Ecology and Hydrology, Huntingdon, 88 p.

- HODGETTS N. & LOCKHART N. 2020. — Checklist and country status of European bryophytes – update 2020. *Irish Wildlife Manuals* 123: 1-214.
- LINDBERG S. O. 1862. — Om ett nytt släkte, *Epipterygium*, bland bladmossorna. Öfversigt af Kongl. Vetenskaps-akademiens förhandlingar 19: 599-609.
- MÄGDEFRAU K. 1982. — Life-forms of bryophytes, in SMITH A. J. E. (ed.), *Bryophyte Ecology*. Chapman and Hall, London: 45-58.
- OCHI H. 1955. — Contributions to the mosses of Bryaceae in Japan. *Journal of Japanese Botany* 30: 87-92.
- SÉRGIO C. & CARVALHO S. 2003. — Annotated catalogue of Portuguese bryophytes. *Portugaliae Acta Biologica* 21: 5-230.
- SHAW A. J. 1984. — Quantitative taxonomic study of morphology in *Epipterygium*. *The Bryologist* 87: 132-142.
- SMITH A. J. E. 2004. — *The Moss Flora of Britain and Ireland*. Cambridge University Press, Cambridge, 1026 p.

*Submitted on 30 October 2021;
accepted on 9 June 2022;
published on 9 November 2022.*