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Pterygoneurum sampaianum (Guim.) Guim.:
range extension to Africa, first mentions in France,
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and improved morphological circumscription

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***Pterygoneurum sampaianum* (Guim.) Guim.:
range extension to Africa, first mentions in France,
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and improved morphological circumscription**

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ABSTRACT

Pterygoneurum sampaianum (Guim.) Guim. is newly recorded in Tunisia and in France. Molecular data from French and Tunisian samples support the specific rank of *P. sampaianum* and allow for a clear differentiation from *P. ovatum* (Hedw.) Dixon in cases where the morphology appears to be transitional between the species. By including a molecular phylogenetic analysis based on the sequence data obtained from European representatives of the genus, we could re-evaluate the phylogenetic affinities of *P. sampaianum* which was found to be close to the recently described *P. papillosum* Oesau. Based on the molecularly guided identifications, we provide an amended detailed description of *P. sampaianum* and report on ecological and chorological details of the newly recorded specimens.

KEY WORDS

Pottiaceae,
chorology,
trnM-trnV,
rps4,
specific status,
new records.

RÉSUMÉ

Pterygoneurum sampaianum (Guim.) Guim. : élargissement de l'aire de répartition à l'Afrique, première mention en France, confirmation du statut spécifique et amélioration de la circonscription morphologique. *Pterygoneurum sampaianum* (Guim.) Guim. est nouveau pour la Tunisie et la France. Une analyse phylogénétique moléculaire réalisée à partir d'échantillons de France et de Tunisie appuie le rang spécifique de *P. sampaianum*, et permet sa nette distinction de *P. ovatum* (Hedw.) Dixon dans les cas où la morphologie semble intermédiaire entre les deux espèces. L'inclusion dans cette analyse de séquences d'autres représentants européens du genre permet la réévaluation des affinités phylogénétiques de *P. sampaianum*, qui apparaît proche du récemment décrit *P. papillosum* Oesau. Nous pouvons ainsi fournir une description détaillée modifiée de *P. sampaianum*, ainsi que des détails écologiques et chorologiques sur la base des données nouvellement obtenues.

MOTS CLÉS

Pottiaceae, chorologie, *trnM-trnV*, *rps4*, statut spécifique, signalements nouveaux.

INTRODUCTION

The genus *Pterygoneurum* Jur. (Pottiaceae) contains ten currently accepted species (<https://www.bryonames.org/nomenclator?group=Pterygoneurum>, accessed on 21 July 2022) distributed on all continents, generally in regions where the climate is arid and semiarid. The genus is well-defined in its gametophytic features, sharing bulbiform, gregarious or cushion-forming plants with concave, often imbricate leaves constituting a photosynthetic chamber housing distinct lamellate expansions on the ventral side of the costa. The sporophyte, on the other hand, is rather variable, most commonly stegocarpous on variously long seta with typically absent peristome (rudimentary peristome present in *P. lamellatum* (Lindb.) Jur.), but cleistocarpous capsules on short seta are developed in *P. kozlovii* Laz. and *P. sibiricum* Otnyukova. Six species are currently recognized in Europe (Hodgetts *et al.* 2020), yet three additional taxa, that were described relatively recently, are now considered to be phenotypes of *P. lamellatum* (*P. compactum* M.J.Cano *et al.*) and *P. ovatum* (Hedw.) Dixon (*P. crossidioides* W.Frey, Herrnst. & Kürschner and *P. squamosum* Segarra & Kürschner) (Guerra *et al.* 2006; Hodgetts *et al.* 2020). Molecular data have never been used to support either the acceptance or the synonymization of the taxa.

Pterygoneurum sampaianum (Guim.) Guim. was described in southern Portugal (Guimarães 1917) and originally considered to be endemic to the Iberian Peninsula, growing typically on saline and gypsum soils. However, Guerra *et al.* (1995a) suggested the synonymy of *P. sampaianum* with *P. cavifolium* var. *muticum* Schiffn., based on a type from Aleppo (Syria), and with *P. cavifolium* var. *humile* J.J.Amann, based on a type from the Swiss Valais. This taxonomic decision considerably enlarged the species' known distribution. Now, according to Hodgetts & Lockhart (2020), the distribution includes Portugal, Spain, the Balearic Islands, Switzerland and Crete in Europe, but is otherwise restricted to the protologue-based single record from Syria mentioned above. The taxonomic status of *P. sampaianum* has often been questioned (Casas & Brugués 1978; Guerra *et al.* 1995a, 2006), given the known morphological plasticity of *P. ovatum*, which appeared to include *P. sampaianum*-like plants.

The authors' recent field surveys in Tunisia and Mediterranean France led to the discovery of several populations of a taxon putatively assigned to *Pterygoneurum sampaianum*. However, some of the observed characteristics did not fit the available descriptions, showing intermediate states between those reported for *P. sampaianum* and *P. ovatum*. The identity of these plants was thus ambiguous in line with the views of Guerra *et al.* (1995a, 2006). We therefore decided to obtain molecular data to resolve the identity of these questionable plants and elucidate the relationship to other *Pterygoneurum* species as well. Currently, some molecular data are available for *P. ovatum*, *P. subsessile* (Brid.) Jur. and *P. lamellatum* (NCBI search for txid200747[Organism:exp] at <https://www.ncbi.nlm.nih.gov/nucleotide/>, accessed on 21 July 2022), but none of the three species have ever been analysed simultaneously with the same set of genomic loci. Having considered the common simultaneous occurrence of phylogenetically unrelated ITS variants in the genomes of multiple representatives of Pottiaceae subfam. Pottioideae, including *Pterygoneurum*, as described by Košnar *et al.* (2012), we opted for the use of the plastid loci *rps4* and *trnM-trnV*, which have been successfully used on previous studies in Pottiaceae (Kučera *et al.* 2013, 2020) and therefore ensure the provision of reasonable phylogenetic context.

MATERIAL AND METHODS

We evaluated the following morphological characteristics in *Pterygoneurum ovatum* and *P. sampaianum*: general habit as observed under the stereomicroscope; subterranean organs (stems and rhizoids), after repeated washing in distilled water to eliminate a maximum of sand and other debris; proximal and distal leaves, carefully detached from the stem with fine tweezers and placed under glass cover and examined under transmitted light microscope; cell width and length taking into account one of the two opposite cell walls; hand-made transverse sections of entire leaves at mid-leaf; capsule shape and size; and spore diameter mounted in tap water.

All *Pterygoneurum ovatum* and *P. sampaianum* specimens listed in the taxonomy section were used for the morphological assessment. Two additional French localities (Isère

TABLE 1. — Voucher information of sequenced specimens and GenBank accession numbers.

Species	Voucher information	<i>rps4</i>	<i>trnM-trnV</i>
<i>Chenia leptophylla</i>	Spain • Murcia, Los Pulpites; <i>J. Kučera 13661</i> ; CBFS.	JX679982	JX679932
<i>Crossidium crassinervium</i>	Spain • Murcia, Los Pulpites; <i>J. Kučera 13662</i> ; CBFS.	Cr1670R	Cr1670M
	Spain • Almería, Tabernas; <i>J. Kučera 17296</i> ; CBFS.	Cr1731R	Cr1731M
<i>Crossidium squamiferum</i>	Montenegro • Virpazar; <i>J. Košnar 1414</i> ; CBFS.	Cr1640R	Cr1640M
	United States • California, San Bernardino Co., Joshua Tree Wilderness; <i>J.C. Brinda 2738</i> ; CBFS (dupl.).	Cr2354R	Cr2354M
<i>Hennediella heimii</i>	Norway • Svalbard, Petuniabukta; <i>J. Košnar 1932</i> ; CBFS.	He571R	He571M
<i>Pterygoneurum kozlovii</i>	Czech Republic • Sedlec, distr. Břeclav; <i>J. Kučera 19418</i> ; CBFS.	Pn1335R	Pn1335M
<i>Pterygoneurum lamellatum</i>	Czech Republic • Čejč; <i>J. Kučera 15594</i> ; CBFS.	Pn1333R	Pn1333M
	Czech Republic • Dolní Kounice; <i>P. Dřevojan PDb18/007</i> ; CBFS.	Pn1726R	Pn1726M
<i>Pterygoneurum ovatum</i>	Czech Republic • Čejč; <i>J. Kučera 15591</i> ; CBFS.	Pn1330R	Pn1330M
<i>Pterygoneurum ovatum</i> (<i>crossidioides</i> morph)	France • Puy-de-Dôme, Veyre-Monton.	Pn1332R	Pn1332M
<i>Pterygoneurum papillosum</i>	United Kingdom • North Somerset, Worley Hill; <i>T.L. Blockeel 44/008</i> ; CBFS (dupl.).	Pn1747R	Pn1747M
	Germany • Rheinland-Pfalz, Wolfshheim; <i>M. Siegel s.n.</i> ; CBFS (dupl.).	Pn1757R	Pn1757M
<i>Pterygoneurum sampaianum</i>	France • Aude, Fitou; <i>V. Hugonnot 21503-2</i> ; CBFS (dupl.).	Pn2358R	–
	France • Pyrénées-Orientales, Serrat de l'Escorpiu; <i>V. Hugonnot 21503-1</i> ; CBFS (dupl.).	Pn2359R	Pn2359M
	Spain • Almería, Fondón; <i>J. Kučera 19418</i> ; CBFS.	Pn1334R	Pn1334M
	Tunisia • Siliana Gov., Sidi Ameur; <i>Ben Osman & Hugonnot TUN2020-2</i> ; CBFS (dupl.).	Pn2357R	Pn2357M
<i>Pterygoneurum subsessile</i>	Czech Republic • Čejč; <i>J. Kučera 15580</i> ; CBFS.	Pn1331R	Pn1331M
<i>Stegonia latifolia</i>	Austria • Salzburg, Mt Hohe Dock; <i>J. Košnar 1448</i> ; CBFS.	Sg1641R	Sg1641M
<i>Syntrichia latifolia</i>	Czech Republic • Mohelno; <i>J. Kučera 18746</i> ; CBFS.	Sy1646M	Sy1646R
<i>Tortula acaulon</i>	Czech Republic • Horní Bojanovice; <i>J. Košnar 317</i> ; CBFS.	Po1637R	Po1637M
<i>Tortula atrovirens</i>	Czech Republic • Nezabudice; <i>J. Kučera 17050</i> ; CBFS.	T1659R	T1659M
<i>Tortula hoppeana</i>	Austria • Salzburg, Mt Waldhorn; <i>J. Kučera 12899</i> ; CBFS.	De1653R	De1653M
<i>Tortula inermis</i>	France • Hautes-Alpes, Saint-Crépin; <i>J. Kučera 13530</i> ; CBFS.	T1667R	T1667M
<i>Tortula lindbergii</i>	Czech Republic • Nové Dobrkovice, distr. Č. Krumlov; <i>J. Košnar 245</i> ; CBFS.	Po1636R	Po1636M
<i>Tortula mucronifolia</i>	Austria • Tyrol, Brandberg, Ahornach; <i>J. Kučera 18916</i> ; CBFS.	T1674R	T1674M
<i>Tortula muralis</i> subsp. <i>muralis</i>	Czech Republic • Studánka, distr. Tachov; <i>J. Košnar 771</i> ; CBFS.	T1717R	T1717M
<i>Tortula muralis</i> subsp. <i>obtusifolia</i>	Romania • Călimani Mts., Mt Lucaciu; <i>J. Košnar 1330</i> ; CBFS.	T1720R	T1720M
<i>Tortula protobryoides</i>	Czech Republic • Horní Němčí; <i>J. Košnar 1245</i> ; CBFS.	Po1638R	Po1638M
<i>Tortula subulata</i>	Czech Republic • Jamolice; <i>J. Kučera 18750</i> ; CBFS.	MN696674	MN696650
<i>Tortula truncata</i>	Czech Republic • Borek, distr. Č. Budějovice; <i>J. Kučera 20869</i> ; CBFS.	Po1723R	Po1723M
	Czech Republic • Velešín, Skřidla; <i>J. Kučera 22437</i> ; CBFS.	Po2030R	Po2030M
<i>Tortula vahliana</i>	Spain • Murcia; <i>J. Kučera 13630</i> ; CBFS.	T1654R	T1654M

department) have been recently found by S. Geoffroy, A. Labroche, Y. Longeot and M. Maglio and the ecological details of these populations have been provided by them to the authors.

The selection for the molecular sampling included four specimens of *Pterygoneurum sampaianum* (two from France, one from Spain, and one from Tunisia), two specimens of *P. ovatum* (with one approaching the morphology described for *P. crossidioides*), two of *P. lamellatum*, two of *P. papillosum* and one each of *P. subsessile* and *P. kozlovii*. To put the selection into a wider phylogenetic context, we added a representative selection of Pottiaceae subfam. Pottiioideae, based on the earlier studies by Werner *et al.* (2002) and Kučera *et al.* (2013). The specimens were sampled for plastid *rps4* and *trnM-trnV* loci in the laboratory of the University of South Bohemia's Faculty of Science, Department of Botany according to the protocols described in Kučera *et al.* (2013, 2019). Table 1 lists the molecularly sampled specimens.

Raw sequence data were checked for sequencing errors and primer complements trimmed in BioEdit v.7.2.5 (Hall 1999) and Geneious Prime 2019 (Biomatters Ltd.,

<http://www.geneious.com/>). The sequences were aligned using the online interface of MAFFT v7.452 (Katoh *et al.* 2019) using the E-INS-i strategy with 200 PAM/ $\kappa = 2$ scoring matrix, gap opening penalty set to 1.53, and off set value set to 0.0. Indel data were scored using the simple indel coding method (Simmons & Ochoterena 2000) and used as a separate partition in the concatenated data matrix.

Bayesian inference (BI) and Maximum Likelihood (ML), partitioned between DNA and indel data, were used for the phylogenetic inference, using the MrBayes v.3.2.7a (Ronquist *et al.* 2012) and RAxML v.8.2.12 (Stamatakis 2014) software packages run at the cluster computer facilities of MetaCentrum VO (see Acknowledgements). Rate variation across sites was set to account for the proportion of invariable sites in BI and the nucleotide evolutionary models were estimated in MrBayes using the sampling across the whole GTR model space (nst = mixed). For ML analysis, the GTR model was used since other complex models are not implemented. We ran the BI in eight chains (one cold, seven heated), setting the temperature experimentally to 0.08. The convergence between runs (set to 0.01) was reached mostly

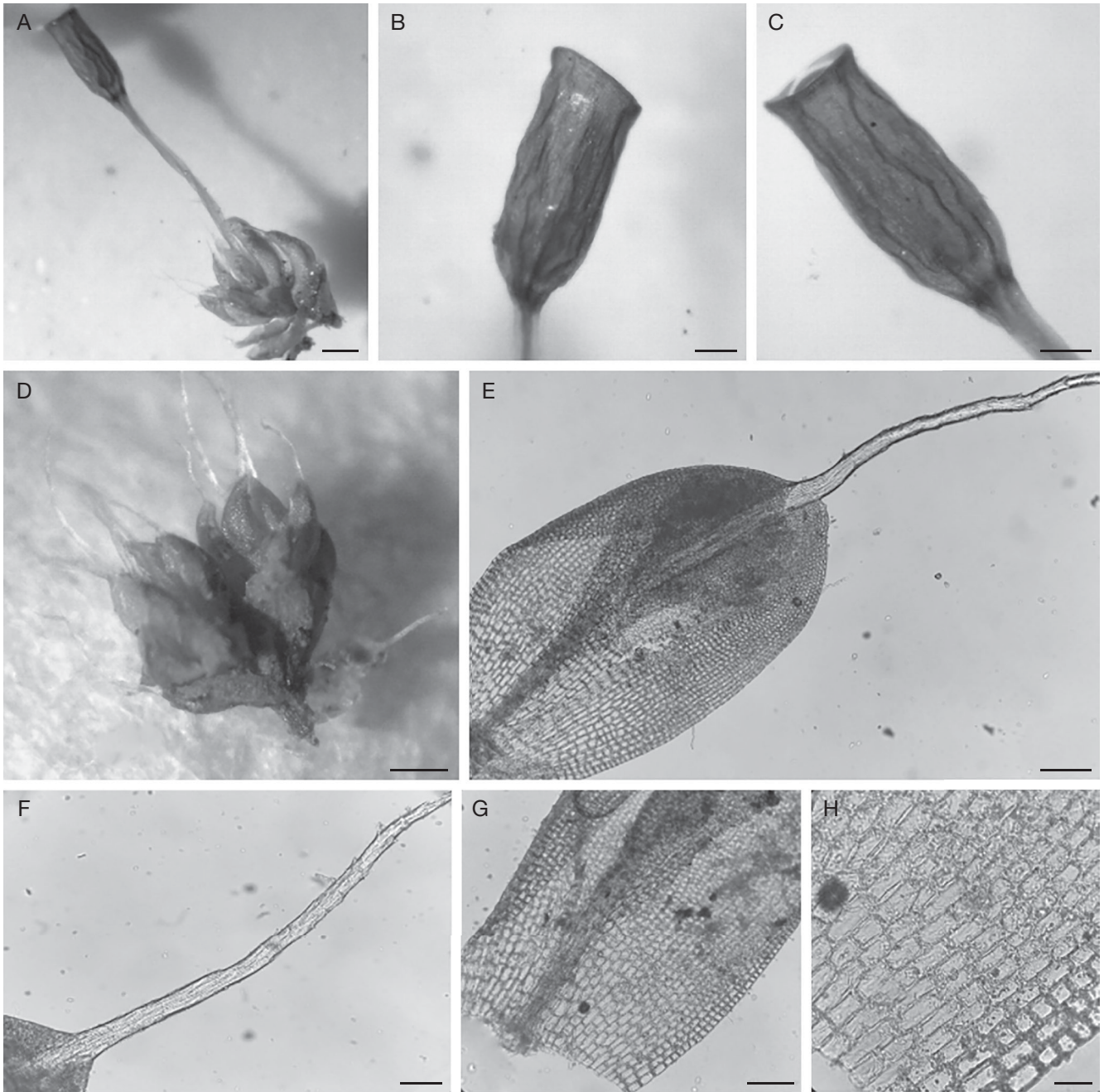


FIG. 1. — *Pterygoneurum ovatum* (Hedw.) Dixon: **A**, habit; **B**, **C**, urn; **D**, gametophyte; **E**, leaf; **F**, hair-point; **G**, leaf base; **H**, marginal areolation at leaf base. Scale bars: A, D, 200 µm; B, C, F, G, 100 µm; E, 300 µm; H, 30 µm.

before 200 000 generations upon several runs, but we allowed the analysis to run for additional two million generations, after which the convergence usually oscillated around 0.005; ESS values were checked using Tracer v1.7 (Rambaut *et al.* 2018). ML analyses were run on an identical matrix, the bootstrap analysis was allowed to stop automatically using the autoMRE command.

TreeGraph 2 (Stöver & Müller 2010) was used to summarize the topology and support from different analyses, and the resulting trees were further edited graphically in Inkscape 1.2 under the GPL license.

RESULTS

The studied morphological characteristics of *Pterygoneurum ovatum* and *P. sampaianum* are compared in Table 2 and the plants are illustrated in Figures 1 and 2.

Based on the results of the phylogenetic analyses (Fig. 3), all analysed species of *Pterygoneurum* were found to form a monophyletic, highly supported clade of Pottiaceae subfam. Pottioideae, and this lineage is nested within a more inclusive fully supported clade containing members of the genera *Tortula* Hedw. *sensu lato* (including *Desmatodon* Brid., *Pottia*

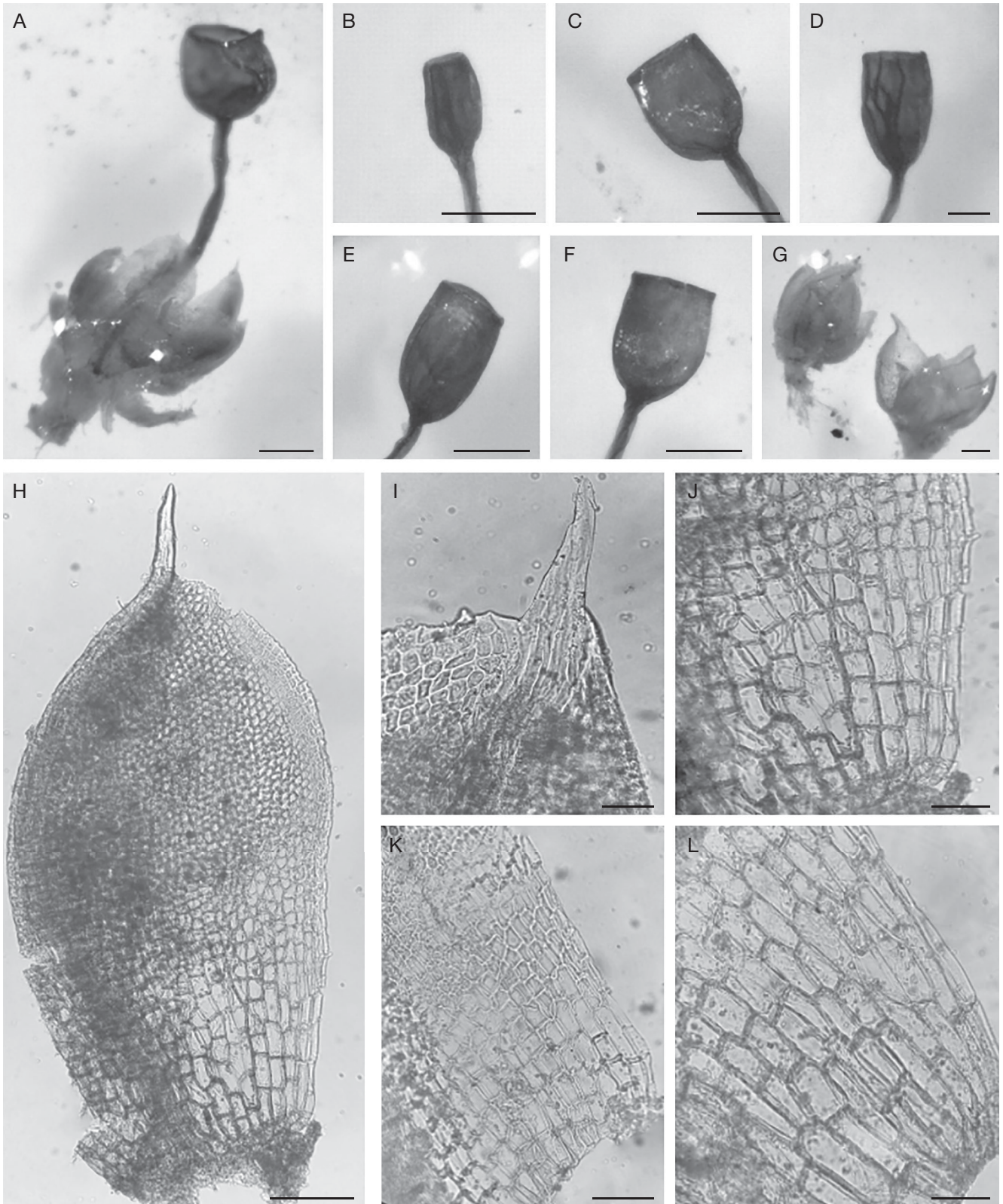


FIG. 2. — *Pterygoneurum sampaianum* (Guim.) Guim.: **A**, habit; **B-F**, urn; **G**, gametophytes; **H**, leaf; **I**, hair-point; **J-L**, marginal areolation at leaf base. Scale bars: A-C, E, F, 200 μ m; D, G, H, 100 μ m; I, J, L, 30 μ m; K, 50 μ m.

Ehrh. ex Fürnr. and *Phascum* Hedw.), *Crossidium* Jur. and *Stegonia* Venturi. In contrast, analysed species of *Tortula* (even after excluding members of *Desmatodon*, *Pottia* and *Phascum*)

and *Crossidium* were not found to receive molecular support as a monophyletic unit. Within *Pterygoneurum*, three well-supported clades without well-resolved mutual affinities were

TABLE 2. — Morphological comparison between *Pterygoneurum sampaianum* (Guim.) Guim. and *P. ovatum* (Hedw.) Dixon.

Morphological characters	<i>Pterygoneurum sampaianum</i> (Guim.) Guim.	<i>Pterygoneurum ovatum</i> (Hedw.) Dixon
Gametophyte		
General habit	Isolated individuals.	Small tufts, or extensive carpets.
Shoot	Shortly bulbiform, <2 mm high.	Stem elongated, 2-7 mm high.
Rhizoids	Less than 10, tuberous, 36-50 µm thick.	Numerous, 25-30 (40) µm wide.
Proximal leaves	Reduced, poorly chlorophyllose and awn-less.	Normal, chlorophyllose, bearing a normal hair-point.
Distal leaves	Deeply concave to convolute, wider than longer; 0.7-0.9 × 0.7-0.8 mm (rarely longer than wider; 0.4-0.5 × 0.8-0.9 mm).	Concave to carinate, not convolute, longer than wide; 0.6-1.2 × 0.8-1.4 mm.
Hair-point	Mostly absent or short, or longer (<400 µm), smooth.	Constantly long (<2500 µm), denticulate in the distal part.
Basal marginal cells	Forming a hyaline border of strongly differentiated cells (longer and thinner) or no border differentiated.	Not forming a border (or marginal cells progressively slightly differentiated).
Basal cells	15-22 × 18-45 µm.	12-21 × 28-71 µm.
Median cells	8-15 × 8-20 µm.	11-18 × 13-35 µm.
Apical cells	Often a majority of cells hyaline, 7-13 × 8-18 µm.	Not hyaline, or a few cells hyaline, 3-12 × 10-15 µm.
Distal margin	Often denticulate.	Entire, or rarely a few denticulations.
Anatomy of nerve	Guide cells poorly differentiated; no hydroids; dorsal stereid poorly differentiated.	3-4 guide cells differentiated; hydroid strand; dorsal stereid poorly differentiated.
Ventral lamellae	2(-3); 5-15 cells high.	2-4; 8-22 cells high.
Sporophyte		
Seta	<2.5 mm.	<3.5 mm.
Theca	Cylindrical to cupulate, <890 µm long; exothecium faintly wrinkled when dry.	Longly cylindrical to ovoid, <2000 µm long; deeply wrinkled with anastomoses when dry.
Spores	35-58 µm across diameter.	23-35 µm across diameter.

discovered; one containing *P. ovatum* (including *P. crossidioides* morph) and *P. lamellatum*, the second containing the species with immersed capsules, *P. sessile* and *P. kozlovii*, and the third including the short-haired species *P. sampaianum* with *P. papillosum*. Interestingly, *P. ovatum* and *P. lamellatum* showed a full sequence identity in analysed regions despite the clear, stark difference in both sporophytic and gametophytic features. Three of the *P. sampaianum* sequences (specimens from France and Spain) are identical in the analysed loci, but the accession from Tunisia differs in one substitution each in the *rps4* gene and *trnV* gene intron. The sequences of *P. sampaianum* and *P. ovatum* differ in five *rps4* gene and two *rps4-trnS* spacer substitutions, three *trnM-trnV* substitutions and four 1-10 bp long indels in *trnM-trnV* part.

DISCUSSION

The results of the molecular analyses fully justify maintaining the specific rank of *Pterygoneurum sampaianum* with respect to *P. ovatum*, a distinction that has been repeatedly called into question with respect to seemingly intergrading morphological features (Guerra *et al.* 1995a, 2006). Contrary to previous suggestions, *P. sampaianum* appears most closely related to the recently described *P. papillosum*, with which it has never been compared (Oesau 2003; Blockeel & Ottley 2015). Yet it shares the rather minute size and occurrence as single, gregarious bulbiform plants, the absence of a well-developed leaf hair-point, and few ventral costa lamellae (two well-developed ones, yet often with an additional smaller lamella). The differences between *P. papillosum* and *P. sampaianum* are quite salient in the dorsally markedly papillose lamina cells, the

lower adaxial lamellae, longer capsules and smaller spores, *c.* 25-40 µm. We looked specifically for the dorsal papillae in *P. sampaianum* but failed to observe any trace of papillosity.

The morphological differentiation of this species from other *Pterygoneurum* species except *P. ovatum* is straightforward, but the variability of some characteristics and the relatively nebulous circumscription of *P. ovatum*, means that the species was not universally accepted. The known variability of *P. sampaianum* should be amended by morphs with longipilose leaves without laminal basal hyaline border and cylindrical capsules.

Well-developed morphs of *Pterygoneurum sampaianum* are immediately distinct, even in the field. Its main characteristics are its very small size (3 mm high, sporophyte included), colonies of isolated plants, and its strongly bulbiform habit with clear distinctions between the basal and median or perichaetial leaves. The distal leaves in *P. sampaianum* are straight, deeply concave to convolute, and resemble the habit of *Stegonia latifolia* (Schwägr.) Venturi ex Broth., whereas they are mostly concave-carinate and slightly twisted (when dry) in *P. ovatum*. In *P. sampaianum*, well-developed leaves are wider than they are long, and at times suborbicular, with expanded shoulders, an indistinct mucro or a short, stout awn or, more exceptionally, longer but completely smooth hair. The leaf margins are denticulate, frequently with geminate teeth in the distal ½. The spores are very large (often near 50 µm). By contrast, *P. ovatum* usually bears a long and prominent hair point that is often denticulate at the apex. Spore size, a definite morphological characteristic, is markedly smaller in *P. ovatum* (25-35 vs 35-58 µm).

Special care should be taken of the commonly occurring mixed stands of *Pterygoneurum sampaianum* with *P. ovatum*, where small, depauperate individuals of the latter may be

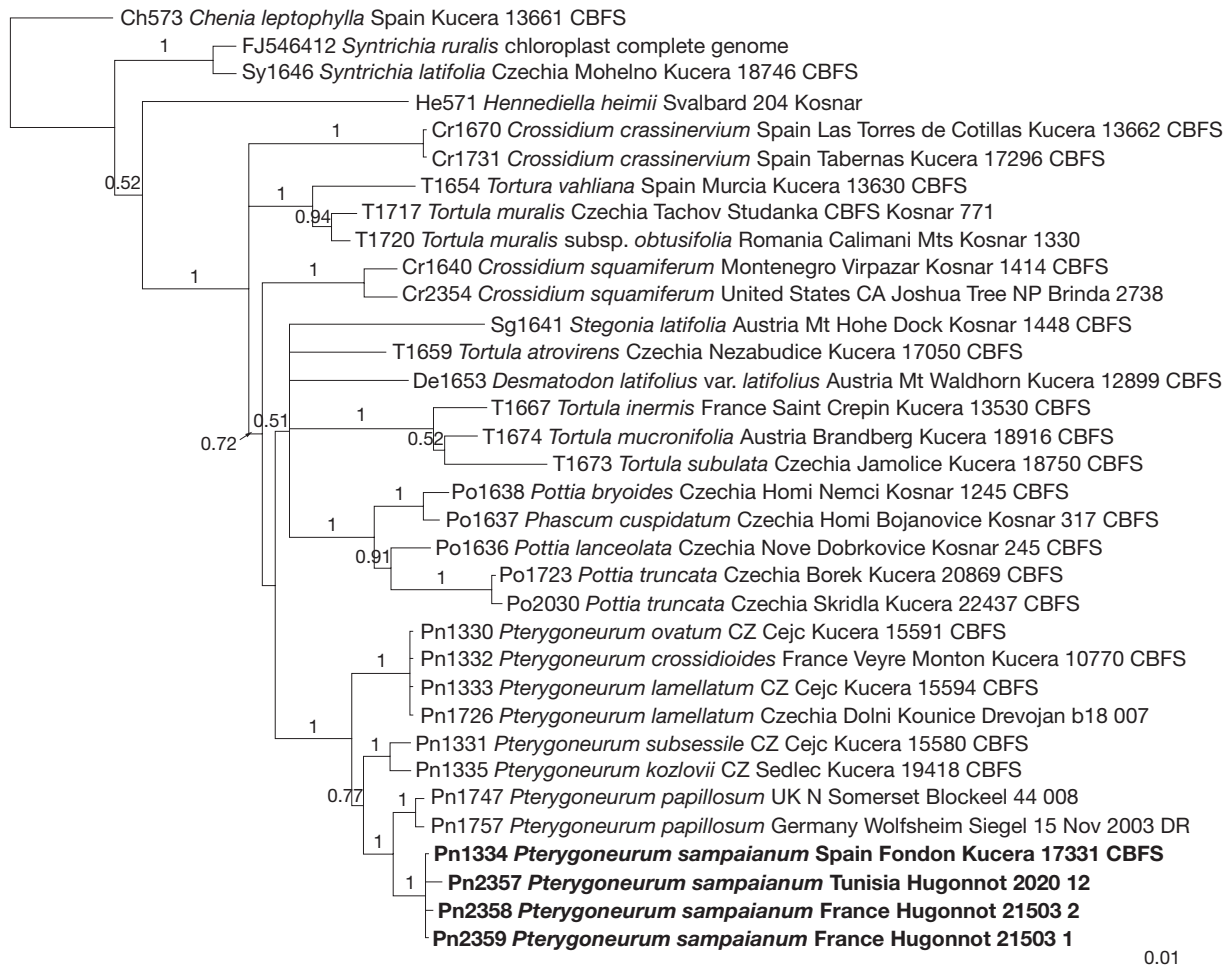


FIG. 3. — Bayesian consensus tree inferred from concatenated chloroplast *rps4-trnS* and *trnM-trnV* sequence data of the analysed dataset of Pottiaceae subfam. Pottiioideae, partitioned between DNA sequence and indel data. Posterior probability from BI is displayed above the branches; bootstrap support (656 replications) from ML analysis is displayed below the branches.

as small as *P. sampaianum*, but whose hairpoint length and spore size differ as described above. Very small and particularly sterile individuals may not be identifiable solely on morphological grounds.

TAXONOMY

Family POTTIACEAE Schimp.
Genus *Pterygoneurum* Jur.

Pterygoneurum ovatum (Hedw.) Dixon

EXAMINED SPECIMENS. — France • Savoie, Aussois, Barmettaz; 45°13'19.6"N, 06°44'54.0"E; 1350 m; 4.III.2021; leg. Hugonnot • Savoie, Val-Cenis, Lanslevillard; 45°16'2.5"N, 06°48'17.5"E; 1360 m; 18.IV.2008; leg. Hugonnot • Hérault, Agde, Notre Dame de l'Agenouillade; 43°17'31.9"N, 03°27'14.0"E; 5 m; 9.II.2002; leg. Hugonnot • Portiragnes, Roquehaute; 43°18'9.7"N, 03°22'13.2"E; 25 m; 15.II.2000; leg. Hugonnot • Haut-Rhin, Westhalten; 47°57'41.6"N, 07°15'20.0"E; 320 m; 12.III.2009; leg. Hugonnot • Haute-Loire, Brives-Charensac; 45°3'6.6"N, 03°56'22.8"E; 700 m; 12.III.2007;

leg. Hugonnot • Puy-de-Dôme, Gimeaux; 480 m; 6.I.2019; leg. Hugonnot • Puy-de-Dôme, Neschers, La Grave; 45°56'40.7"N, 03°5'9.5"E; 400 m; 6.I.2019; leg. Hugonnot • Puy-de-Dôme, Chateaugay; 45°51'12.8"N, 03°5'57.9"E; 380 m; 6.I.2019; leg. Hugonnot • Puy-de-Dôme, Chateaugay; 45°51'16.3"N, 3°6'13.6"E; 410 m; 6.I.2019; leg. Hugonnot • Cantal, Massiac, Saint Victor; 45°15'47.5"N, 03°11'10.2"E; 708 m; 18.V.2002; leg. Hugonnot. Spain • Torroella de Montgrí, L'Estartit, Cap Castell; 42°4'44.5"N, 3°11'41.1"E; 12.II.2020; leg. Hugonnot. Tunisia • Tunisian Dorsal, Drija valley; 36°06'58.6"N, 09°39'27.8"E; 490 m; 10.III.2020; leg. Ben Osman & Hugonnot; TUN2020-53 • Tunisian Dorsal, Henchir el Bez; 36°00'23.9"N, 09°32'50.1"E; 635 m; 11.III.2020; leg. Ben Osman & Hugonnot; TUN2020-54 • Tunisian Dorsal, Kesra-Plateau; 35°48'59.7"N, 09°21'47.4"E; 1040 m; 11.III.2020; leg. Ben Osman & Hugonnot; TUN2020-152 • Tunisian Dorsal, Jbel Bargou; 36°01'50.4"N, 09°36'30.1"E; 670 m; 12.III.2020; leg. Ben Osman & Hugonnot; Vincent Hugonnot's personal herbarium.

Pterygoneurum sampaianum (Guim.) Guim.

EXAMINED SPECIMENS. — Tunisia • Tunisian Dorsal, Siliana Governorate, Delegation of Makthar, Sidi Ameur, site 2020-12;

35°52'47.46"N, 09°28'23.24"E; 710 m a.s.l.; 11.III.2020; leg. Ben Osman & Hugonnot; TUN2020-2.

France • Pyrénées-Orientales, Opoul, Crest del Camp de l'Auca; 42°51'55.74"N, 02°54'1.22"E; 190 m; 6.III.2020; leg. Hugonnot • 42°51'49.52"N, 02°53'39.38"E • Aude, Fitou, Les Courtiels; 40°53'0.83"N, 02°57'41.28"E; 170 m; 6.III.2020; leg. Hugonnot • Savoie, Aussois, Maurienne valley, Barmettaz; 45°13'12.23"N, 06°44'49.82"E; 1300 m; 4.III.2021; leg. Hugonnot.

Spain • Torroella de Montgrí, L'Estartit, Cap Castell; 42°4'44.5080"N, 03°11'41.1360"E; 12.II.2020; Vincent Hugonnot's personal herbarium • Andalucía, Almería, Fondón, Sierra de Gádor, Barranco de Cacín; 36°58'49.1"N, 02°48'46.7"W; c. 800 m; 28.IV.2015; leg. J. Kučera; CBFS 17331, 17332.

EMENDED DESCRIPTION

Previous morphological descriptions did not fully account for the morphological variability observed in the studied specimens whose identification was confirmed using molecular data. We therefore provide an emended morphological description of *Pterygoneurum sampaianum*.

Plants gregarious, in loose colonies characteristically consisting of very small sterile individuals and much larger fertile individuals, shortly bulbiform, whitish green to pale green, often with discolored tips, 1.25–1.8 (3.5) mm high. Axillary hairs 3–4 in axils of upper leaves, 9–12 × 100–130 µm, made of 1–2 basal cells short and 3–5 feebly colored and longer cells; terminal cell 9–10 × 30–35 µm. Subterranean part of stem thick and brown, 0.19–0.24 × 0.45–0.55 mm, of thick-walled cells, with or without 1–2 non-chlorophyllous scales, proximally attached to substrate by 5–10 large brown rhizoids, 36–50 µm wide near base, often more than 6 mm long, ramified, strongly decreasing in size towards the apex (to 8 µm wide) and becoming hyaline, smooth but coated with fine soil material. Leafy stem aerial, unbranched or occasionally branched (often the smaller branch sterile, reduced to few leaves), with cortex undifferentiated (externally with smaller cells with barely thickened walls), central strand present but weak, of several cells. Proximal above-ground leaves reduced and hardly chlorophyllose, equally wide or wider than long, trapezoidal, suborbicular to rectangular, deeply concave, with none or very short acumen, awnless; basal marginal cells strongly differentiated into 2–4 cell-wide hyaline border, of long rectangular cells (5–7 × 40–50 µm), ascending along the margin; median and apical cells often very thick-walled. Distal leaves erect, deeply concave to convolute, awnless or with short straight hyaline smooth awn (70–100 µm long), individual leaves on some shoots occasionally bear a longer, up to 400 µm long, at times even flexuous hair, or many leaves piliferous on the same shoot; leaves wider than long, trapezoidal, 0.7–0.9 × 0.7–0.8 mm, rarely longer than wide 0.4–0.5 × 0.8–0.9 mm, widely rounded to truncate at apex, with plane margins; basal marginal cells forming a more or less distinct hyaline border, 3–6 cells wide, ascending to apical 1/3 of rectangular cells 10–14 × 40–70 µm, border totally missing at times; basal cells short-rectangular to quadrate, 15–22 × 18–45 µm; median cells quadrate to rectangular, 8–15 × 8–20 µm; apical cells rounded quadrate to rounded rectangular, 7–13 × 8–18 µm, with thick walls, often hyaline; margin dentate from mid-leaf to apex, teeth formed by the

protruding cells, often geminate. Costa 45–66 µm wide at base, adaxially expanded into 2–3 large lamellae to 15 cells high, running from base to apex, crenulated at margin by protruding conical cells (apex mamilla like, rarely with two mamilla-like ornamentations); terminal cells of lamellae 12–14 × 15–18 µm; surface of lamellae occasionally with short outgrowths of conical cells or small laminal outgrowths; cells of lamellae 14–20 × 18–30 µm; surface cells of costa thick-walled both abaxially and adaxially; abaxial walls of lamina cells more thickened than adaxial ones in transverse section, costa with 2–3 poorly differentiated guide cells, dorsal stereid layer not developed. Autoicous, male buds at stem base on ground level.

Sporophyte with red-brown urn. Seta 0.076 × 0.09 × 1.4–2.5 (3) mm, dextrorse; epidermal cells 8–13 × 18–57 µm, with slightly thickened walls. Seta in transverse section with one layer of epidermal cell with outer tangentially thickened walls, central strand present. Urn shortly cylindrical, rarely cupulate, with faint longitudinal plicae when dry, wide-mouthed, 320–600 × 740–890 µm; exothecial cells irregularly rectangular, 18–32 × 40–87 µm, with rather thin walls. Epidermal cell transverse section with tangentially not or very weakly thickened outer walls. Stomata 1–2, phaneroporos, at base of urn. Annulus poorly differentiated, of 1–2 rows of rectangular, barely vesiculose cells. Mouth with no trace of peristome (either at rim or in the operculum). Operculum with short and blunt beak, 0.40–0.65 mm long. Spores spherical, 35–58 µm across diameter, often ellipsoid or potato-shaped. Calyptra narrowly cylindrical at first, at maturity cucullate, rostrate, subobtuse at apex, covering urn at length (0.4–0.7 mm long).

HABITAT

Our observations allow us to identify the ecological requirements of *Pterygoneurum sampaianum*. The species is typically found in arid or semiarid climates. In the Maurienne valley of the French Alps, the locality is recognized as being among the driest in France, with an average annual rainfall of 518 mm/year, with the vegetation referred to as *Festucetalia valesiacae* Br.-Bl. & Tüxen ex Br.-Bl. 1949. The dominants include *Festuca valesiaca* Schleich. ex Gaudin, *Stipa capillata* L., *S. eriocaulis* Borbás, *Euphorbia seguieriana* subsp. *loiseleurii* (Rouy) P.Fourn., *Koeleria vallesiana* (Honck.) Gaudin and *Galium pusillum* L. In the Isle-Crémieu, North Isère, France (Vénérieu, Simiaud and La Chanas; derelict marl quarry; 45°39'43"N, 05°17'17"W, 45°39'36"N, 05°17'17"W, 45°39'18"N, 5°16'33"W; 238 and 218 m a.s.l.; 3 March 2023; obs. S. Geoffroy, A. Labroche, Y. Longeot and M. Maglio) a calcareous plateau with an average annual rainfall much higher, of 950–970 mm/year, the vegetation where *P. sampaianum* have been spotted is a mosaic of mesoxerophilous grasslands of *Tetragonolobum maritimi*-*Bromenion erecti* J.-M.Royer 2006 and *Teucrium montani*-*Bromenion erecti* J.-M.Royer 2006 and thermophilous semi-wet meadows with *Molinia caerulea* (L.) Moench (*Deschampsia mediae*-*Molinienion arundinaceae* B.Foucault 2008) developed on outcrops of marl-limestone soil with temporary hydromorphy. In the eastern Pyrenees, the average annual rainfall is approximately 550 mm/year. The vegetation

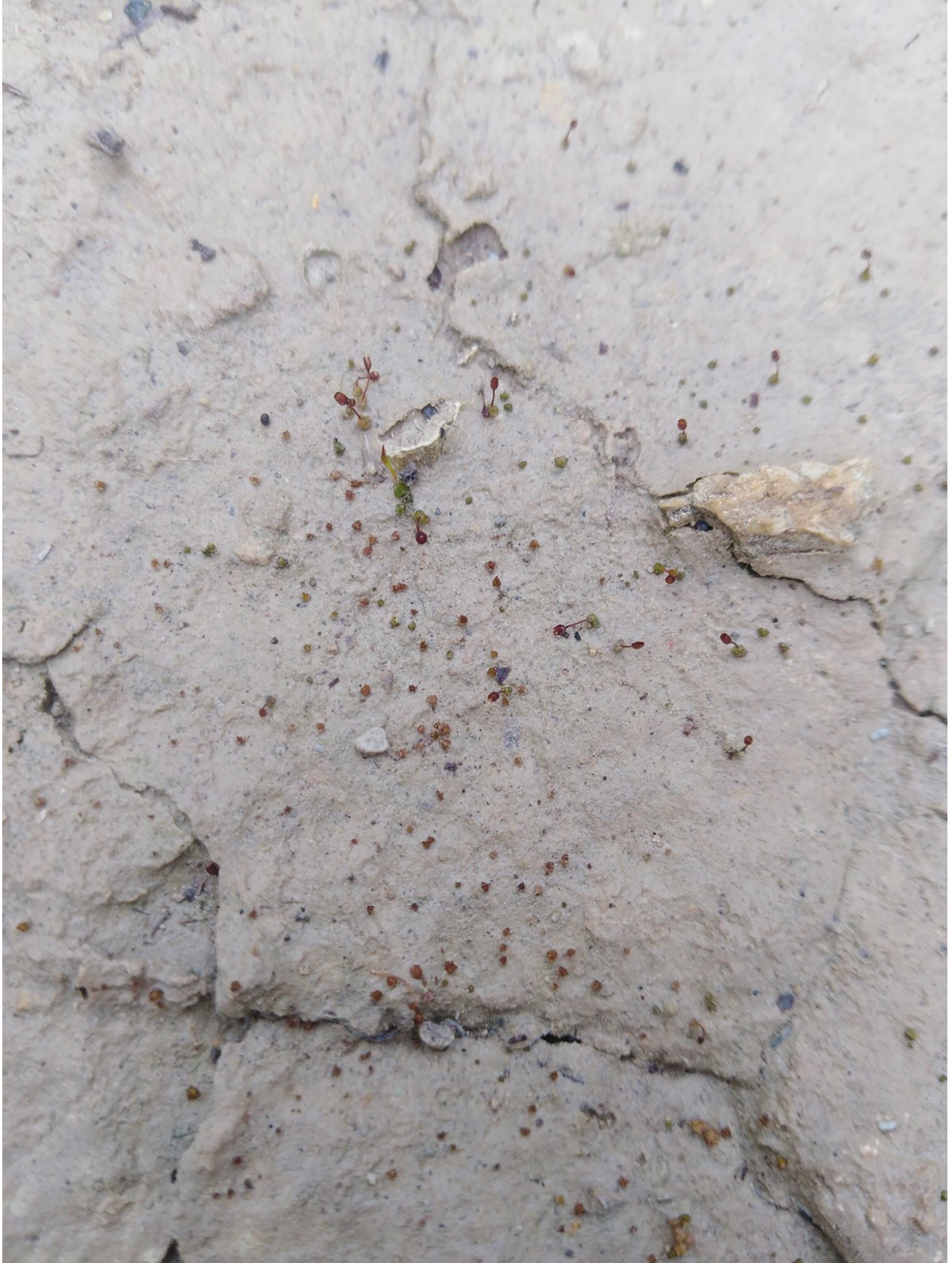


FIG. 4. — Habitat of *Pterygoneurum sampaianum* (Guim.) Guim. (11 March 2020, Tunisia, Siliana Governorate, Sidi Ameur).

comprises degraded grasslands and garrigues with *Brachypodium retusum* (Pers.) P.Beauv., *Rosmarinus officinalis* L., and is referred to the alliances *Phlomidio lychnitidis-Brachypodium retusi* (Rivas-Martínez 1978) Mateo 1983 and *Rosmarinion officinalis* Br.-Bl. ex Molinier. In Tunisia, *Pterygoneurum sampaiianum* was collected from the Tunisian Dorsal, which has an average annual rainfall of c. 400 mm/year. The plants were growing in low matorral vegetation composed primarily of solitary *Pinus halepensis* Mill. and *Quercus ilex* L. subsp. *balota* (Desf.) Samp., with *Cistus clusii* Dunal, *C. creticus* L., *Rhamnus lycioides* L. and *Rosmarinus officinalis*, belonging to the order *Pistacio-Rhamnietalia alaterni* Rivas-Martínez 1975 and the recently described alliance *Loto dorycnium-Pinetum halepensis* Djebaili 2017 (Meddour *et al.* 2017).

In the newly-discovered French populations, the species grows with rich assemblages of pioneer, mainly ruderal bryophytes, often belonging to the family Pottiaceae. In Savoy, the most frequently associated species are *Aloina aloides* (W.D.J.Koch ex Schultz) Kindb., *Bryum dichotomum* Hedw., *Didymodon acutus* (Brid.) K.Saito, *Streblotrichum convolutum* (Hedw.) P.Beauv and *Tortula atrovirens* (Sm.) Lindb. In Isère, main associated species are *A. aloides*, *A. ambigua* (Bruch & Schimp.) Limpr., *Microbryum curvicollellum* (Hedw.) R.H.Zander, *Pottiopsis caespitosa* (Brid.) Blockeel & A.J.E.Sm., *Ptychostomum imbricatulum* (Müll.Hal.) Holyoak & N.Pedersen, *Tortula caucasica* Broth., *T. lindbergii* Broth. and *T. truncata* (Hedw.) Mitt. In the Mediterranean localities they are *Acaulon triquetrum* (Spruce) Müll.Hal., *Aloina aloides*, *Bryum dichotomum*, *B. gemmilocens* R.Wilczek & Demaret, *Didymodon acutus*, *Microbryum curvicollellum* and *M. davallianum* (Sm.) R.H.Zander. Poorer communities are generally dominated by scarce individuals of only two species, *Bryum dichotomum* and *Streblotrichum convolutum*. In Tunisia, the species grows mostly without direct associates. In Andalucía, *P. sampaiianum* grew in fissures of exposed conglomerate rock outcrops, and notable associated species included *Aloina aloides*, *Campylostelium pitardii* (Corb.) E.Maier, *Crossidium aberrans* Holz. & E.B.Bartram, *Didymodon acutus* (Brid.) K.Saito, *D. desertorum* (J.Froehl.) J.A.Jiménez & M.J.Cano, *Encalypta vulgaris* Hedw., *Entosthodon muhlenbergii* (Turner) Fife, *Pseudocrossidium revolutum* (Brid.) R.H.Zander and *Tortula atrovirens*.

Most significantly, *Pterygoneurum sampaiianum* generally occurs in very open micro-communities (Fig. 4), with low cover of vegetation, and very sparse bryophytes, which strongly suggests a high sensitivity to competition. Although this is a generally well-known trait of Pottiaceae communities, the species' apparent inability to invade more closed populations of larger species in the immediate vicinity appears to be significant. In the Pyrénées-Orientales and in Aude (France), the species is strongly dependant on repeated trampling of paths in limestone plateaus where it grows in linear populations on a restricted fringe at the transition between small grassland communities and totally bare substrate (corresponding to car tracks or hiking paths).

The general association of *Pterygoneurum sampaiianum* with fine clay and constraining substrates is also important. Initially it was believed to grow on the chalk clay of the Algarve

(Guimarães 1917) and on gypsiferous or saline soils in SE and NE Spain (Guerra *et al.* 1995b). Casas & Brugués (1978) describe the microhabitat as a fine layer of clay deposited in the depressions. In Tunisia, the species is strongly linked to degraded habitats, mainly the flanks of small mountainous systems where fluvial flows during violent storms can carve rills and shape badlands characteristic of severely eroded soils. Important quantities of very fine-grained detritic "glacis" accumulate at the foot of the slopes, periodically regenerating new bare habitat suitable for the most diminutive Pottiaceae species.

An examination of the subterranean system of *Pterygoneurum sampaiianum*, made of large and thick-walled rhizoids (compared to the significantly thinner rhizoids of *P. ovatum*) anchored to semi-buried succulent stem, suggests that it could be linked to perennation. In the allegedly short-lived *Acaulon triquetrum*, long-term monitoring allowed Ahrens (2003) to uncover the species' remarkable persistence which turns out to be pauciennial instead. This calls for further studies of similar small pottiaceous mosses since our knowledge of their biology is based on generalizations that do not seem to hold up with a careful individual examination.

CONSERVATION STATUS

The new data on *Pterygoneurum sampaiianum* require to address the possible adjustments to its so far estimated conservation status. Based on the rare occurrences recorded so far in Europe, the species was evaluated as Near Threatened in the last version of European Red List of Mosses (Sérgio & Cano 2019). This assessment has probably mainly been based on the situation in Spain where it is assessed as Least Concern (Brugués & González-Mancebo 2012), as elsewhere in its distribution area, the species was evaluated as Regionally Extinct (RE) in Portugal and Data Deficient in Switzerland (Hodgetts & Lockhart 2020). With the now more accurate morphological circumscription and better knowledge about its habitat in the Mediterranean region, additional records can be expected in the near future. However, vast areas of apparently favourable habitats that do not seem to be occupied by *P. sampaiianum* exist in the Mediterranean. Considering the species' apparent weakness in competition, ecological specialization, and apparent rarity, its threat status cannot currently be lowered but rather, it can be discussed to be evaluated as Vulnerable with respect to the population size which nearly certainly is smaller than 10 000 mature individuals and small individual populations hardly exceeding one hundred individuals in conjunction with the possibly decreasing overall size based on the suitable habitat degradation in the future risk assessment. Therefore, conservation efforts should focus on preserving the habitats where *P. sampaiianum* occurs, ensuring the survival of this species for future generations.

CONCLUSION

The confirmation of the specific status of *Pterygoneurum sampaiianum* conforms to the general trend of the last years

supported by the molecular data, which shows that some taxa should be recognized despite observed morphological transitions between them. Each case should nevertheless be considered individually. The amendment of morphological description now enables a safer differentiation from the morphologically similar common species, *P. ovatum*.

The new data on *Pterygoneurum sampaianum* show that the species has a wider, albeit still restricted, generally Mediterranean distribution in Europe (Portugal, Spain, France, Switzerland and Crete), North Africa (Tunisia) and Middle East (Syria). New records can particularly be expected in the insufficiently explored region of Near East and North African countries.

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