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Article *in* Nova Hedwigia · January 2019

DOI: 10.1127/nova_hedwigia/2019/0564

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Nova Hedwigia, Vol. 110 (2020), Issue 1-2, 79–89 **Article**
Published online December 3, 2019; published in print February 2020

The enigmatic moss *Fissidens jansenii* Sérgio & Pursell recorded on Plateau de Millevaches (Limousin, France) with comments on its morphological variability

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With 3 figures and 1 table

Abstract: The rare *Fissidens jansenii* Sérgio & Pursell is reported on plateau de Millevaches, Limousin (France), nearly 1000 km north of the nearest known population. As a result, *F. jansenii* is known from the Iberian Peninsula and now from western France. An updated distribution map of the species in Europe is provided. The new material is fully described and illustrated and the ecology in France is outlined. Gametophytically, French specimens of *F. jansenii* do not deviate significantly from Portuguese material and the variability of characters is discussed. In France, on plateau de Millevaches, *F. jansenii* is relatively frequent but constitutes rather small populations, with a low number of individuals. Sporophytes were regularly encountered and reproduction is most likely to be by spore dispersal. On plateau de Millevaches, *F. pusillus* (Wilson) Milde shares a comparable habitat but is easily distinguished from *F. jansenii*. Morphologically similar species occurring in Western Europe and that could potentially be confused with *F. jansenii* (*F. rivularis* and *F. rufulus* Bruch & Schimp.) are compared.

Key words: *Fissidens jansenii*; France; geographical distribution; morphological variability; plateau de Millevaches; reproduction

Introduction

Fissidens Hedw. is a taxonomically difficult genus with a particularly high level of morphological variation whose origin remains mostly unexplored (Bruggeman-Nannenga 1982). This is particularly true for species pertaining to the *Pachylomidium* Müll.Hal section where species boundaries are not as sharp as one would expect (Bruggeman-Nannenga 1985). In France, this complex has been the subject of taxonomic study (Pierrot 1975, 1977) but in spite of this, species delimitation often remains ambiguous.

 DOI: 10.1127/nova_hedwigia/2019/0564 www.borntraeger-cramer.de 0029-5035/2019/0564 $ 2.75

Fissidens jansenii Sérgio & Pursell is a species recently described from Portugal where it is only recorded from its type locality, Poço do Inferno, a well-known waterfall in Serra da Estrela (Sérgio & Pursell 2001).

A small *Fissidens* of the section *Pachylomidium* was recently collected from oligotrophic rivulets on Plateau de Millevaches, France, which we determined as *F. jansenii*. An examination of type material confirmed this view. French material was sent to Ron Porley and Ida Bruggeman-Nannenga and both concurred with our morphological identification.

The species was found to be relatively frequent there and with sporophytes which allowed a detailed examination of morphological and reproductive features. Since the species is still poorly-known among bryologists, and particularly because the original description was based on scanty material, we provide a full description of the French plants. Comments on its morphological variability and distinction from related species are provided, and its ecology and distribution are reviewed.

Nomenclature

The nomenclature of species follows Ros et al. (2007) for liverworts and Ros et al. (2013) for mosses.

Results

Selected French specimens examined: France: Nouvelle-Aquitaine (ex Limousin), Creuse, Gentioux-Pigerolles, Les Prades, 750 m a.s.l., 30 August 2016, 1°59’13.78” E, 45°46’13.1” N; Hugonnot (Herbarium V. Hugonnot and PC); Creuse, Bugeat, bois du Citaire, 687 m a.s.l., 25 October 2016, 1°56’15.5” E, 45°36’56.54” N; Hugonnot (Herbarium V. Hugonnot and PC); Corrèze, Peyrelevade, Les Bondes, 750 m a.s.l., 31 August 2016, 20°1’18.87” E, 45°41’55.03” N; Hugonnot (Herbarium V. Hugonnot and PC); Corrèze, Tarnac, Le Moulin du Tailleur, south of locality, 710 m a.s.l., 15 September 2016, 1°56’30.86” E, 45°40’9.66” N; Hugonnot (Herbarium V. Hugonnot and PC). A complete list of new localities is available from the author upon request.

Other specimens examined: Portugal, Beira Alta, Serra da Estrela, Poço do Inferno. Por baixo da ponte. Fissuras das rochas, 1100 m a.s.l., C. Garcia & C. Sérgio (Isotype, LISU 180673).

An up-dated distribution map is provided (Fig. 1). The French localities are about 990 km distant from the Portuguese locality.

Habitat in France: All known populations of *Fissidens jansenii* occur on Plateau de Millevaches (Corrèze, Creuse and Haute-Vienne departments). A shallow dome, deeply dissected by streams and rivers, Plateau de Millevaches is the visible remnant of a large lens-shaped mass of granite, believed to be the result of an intrusion of igneous material

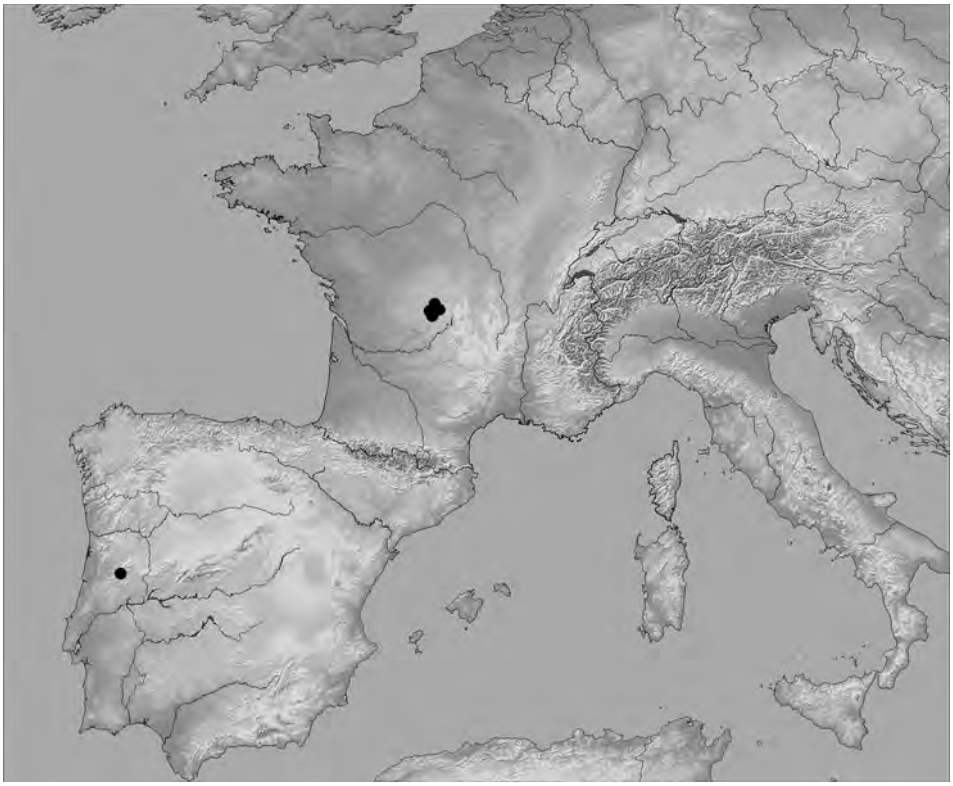

Fig. 1. Known distribution of *Fissidens jansenii*.

in the late Hercynian orogeny. The highest peak of the plateau is Mont Bessou (976 m), at the southern edge of the massif.

The plateau is a patchwork of woodland (mostly non-native coniferous forests) and meadows. The area is famous for the large area covered by bog vegetation. The Vienne River, which has its source here, flows mainly northward. The Vézère River, which arises adjacent to it, drains south into the Dordogne River. Plateau de Millevaches is a typical Oceanic mountain system. It is a rather cold and snowy region. Annual rainfall reaches 1400 mm at the western border and 1100 mm at the eastern limit of the Plateau.

Fissidens jansenii is a hydrophilous moss that seems to tolerate only short periods of desiccation. It is an amphibious species of small acidic watercourses in moderate or pronounced shade. It grows in a low-down zone which is often and persistently submerged. The elevations of the localities range from 675 to 800 m. The bedrock of the area is entirely granitic and the species is markedly acidophilic. It occurs as pure stands in small bare rock fissures where it is firmly anchored by its rhizoids. Exceptionally *Fissidens jansenii* was observed growing at the base of *Alnus glutinosa* Gaertn. Colonies of *F.*

Fig. 2. Colony of *Fissidens jansenii* on granitic rock (width of photograph: 4 cm).

jansenii are always very small, attaining a few cm² at each occurrence. Patches are mostly several metres distant from each other.

Fissidens jansenii is a pioneer moss, always occurring on bare rock surfaces (Fig. 2) and most often found without any immediate associate. It strictly avoids patches of robust bryophytes and is intolerant of competition. It was frequently observed on vertical or even under overhanging rocks. Such surfaces are not liable to accumulate granitic sand which is favourable to more robust bryophytes that develop subterranean shoots such as *Hyocomium armoricum* (Brid.) Wijk & Margad. and *Marsupella aquatica* (Lindenb.) Schiffn.

The bryoflora of such rivulets is often sparse and patchy. Associated species include *Chiloscyphus polyanthos* (L.) Corda, *Dichodontium pellucidum* (Hedw.) Schimp., *Hyocomium armoricum*, *Fissidens pusillus* (Wilson) Milde, *Fontinalis squamosa* Hedw., *Hygrohypnum ochraceum* (Turner ex Wilson) Loeske, *Marsupella aquatica*, *Racomitrium aciculare* (Hedw.) Brid., *Scapania undulata* (L.) Dumort., *Schistidium rivulare* (Brid.) Podp., *Sciuro-hypnum plumosum* (Hedw.) Ignatov & Huttunen. The bryophyte community is assigned to the *Racomitrion acicularis* v. Krus. 1945, a typical alliance of montane streams on non-calcareous rocks. It shows some affinities to *Brachythecietum plumosae* v. Krus. ex Phil. 1956 but further phytosociological study would possibly reveal other original communities.

Description of French material (Fig. 3): *Plants* 2–9(–12) mm long, green in younger parts, blackish in older parts, mostly unbranched or innovating below inflorescences, with 1–3 branches, from distal to proximal half of stem. *Stem* cortex with 2–3 layers, medulla 2–4 layers and a central strand of 4–8 smaller cells. *Rhizoids* at base of stem and at base of innovating distal branches, brownish-red. *Axillary hairs* numerous in each leaf axil, hyaline, comprise 2–4 cells, 60–130 µm long. *Leaves* in 8–12 pairs per stem, erect,

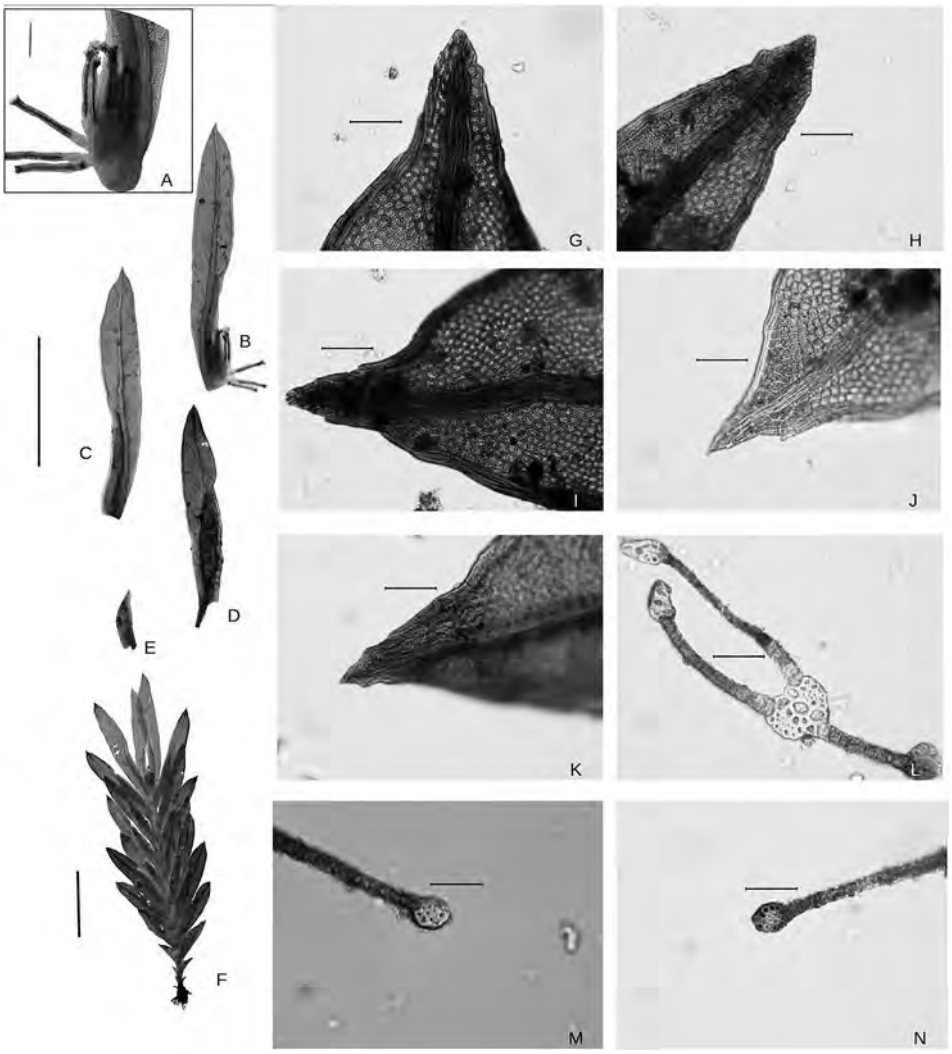

Fig. 3. *Fissidens jansenii*. A: Archegonial bundle (scale bar: 20 µm); B: Terminal leaf; C: Subterminal leaf; D: Vegetative leaf; E: Basal leaf; F: Female individual (scale bar for B–F: 1 mm); G–K: Leaf apices; L: Leaf transverse section; M, N: Limbidium transverse sections (scale bar for G–N: 50 µm).

rigid, oblong-lanceolate to narrowly lanceolate, 2–2.5 × 0.35–0.38 mm, curled to twisted when dry. Lamina occasionally bistratose in patches (mostly on vaginant laminae). *Margin* without teeth but sinuous from the base of leaf, with a continuous strong limbidium, 3–5 cells wide on dorsal laminae, 18–22 µm wide, 7–9 cells wide on vaginant laminae, 2–5 cells thick, 35–42 µm wide, in transverse section circular to elliptical-oblong; limbidium not reaching base of dorsal lamina and not reaching apex of leaf and not confluent with nerve; a zone of 6–8 ovate or linear-vermicular cells occasionally forming a mucro. *Nerve* in transverse section bryoides-type, 50–60 µm wide at base, not reaching apex, ending a few cells below apex or occasionally percurrent or excurrent as a mucro to 40 µm long (in apical leaves). *Vaginant lamina* reaching 1/2–2/3 of leaf-length, acute. *Dorsal lamina* narrowing at base, without intralaminar limbidium, cells firm-walled, hexagonal, 8–12 × 6–9 µm. *Dioicous*, with stem ending either in numerous archegonia or in a group of several antheridia; occasionally synoecious, antheridia mixed with numerous archegonia; antheridia infrequently found naked in axils of stem leaves, rarely with one archegonia. *Paraphyses* lacking. *Perichaetial* leaves narrower than vegetative leaves, apex bluntly acute to obtuse-mucronate or mucronate, vaginant lamina reaching 1/2–2/3 of leaf-length, the two parts unequal. *Sporophyte* solitary, seta 2–4 mm long, theca curved, slightly oblique, oblong to ovoid, 0.4–0.6 mm long, operculum bluntly rostrate, (280–) 400–640 µm long, exothecial cells oblong-rectangular to short-rectangular to quadrate, (14–)25–30 × 14–15(–20) µm, with slightly thickened walls lacking trigones. *Peristome* bryoides-type, thin transverse basal trabeculae, apical oblique and intermingled crests; teeth with 3–4 trabeculae at base, 40–50 µm wide at base, 250–260 µm long. *Calyptra* cucullate, brown with a rusty apex, long rostrate, 630 µm long, covering entire rostrum, with remnant of archegonial neck at apex. Cells of calyptra 17–43 × 6–11 µm. *Spores* smooth, 12–17 µm, greenish.

Reproductive characters: No autoicous individuals (antheridia in small compact buds in the axils of lower leaves) were observed in French populations. Antheridia are mostly grouped in terminal inflorescences, but occasionally are mixed with numerous archegonia constituting a synoicous inflorescence. In spite of this sexual plasticity, male shoots are always found in the immediate vicinity of archegonia, making a network of densely intricate gametangial axes. Sporophytes were frequently seen in almost all sub-populations, but are not abundant, occurring in limited numbers at each location. No asexual propagules (gemmae, tuber) were found.

Discussion

Fissidens jansenii is a poorly known species that has remained somehow enigmatic since its inception almost 20 years ago. César Garcia (pers. comm.) found new populations downstream to Poço do Inferno at other points along the river bed. The recent discovery of a cluster of sub-populations on Plateau de Millevaches firmly anchors the species in the European bryoflora and enables amplification of its morphological differentiation from similar species.

On plateau de Millevaches, *Fissidens jansenii* is frequently associated with *F. pusillus*. In fact, both species shares a comparable habitat and occurs occasionally as mixed stands. In the field small individuals of *F. jansenii* can be difficult to separate from *F. pusillus*; transverse sections of leaves will decide: the limbidium is unistratose (to bistratose) in *F. pusillus* vs. consistently pluristratose in *F. jansenii*.

In western Europe *Fissidens jansenii* could also be confused with *F. rivularis* and *F. rufulus*. The main differentiating characters of these three species are presented in Table 1. Morphologically, *F. jansenii* is best characterized by the following combination of characters: leaves linear-lanceolate, cuspidate; limbidium of vaginant lamina to 37 µm (or more); nerve mostly ceasing below apex; limbidium generally not reaching apex; perigonia never axillary; bistratose patches in vaginant and dorsal lamina.

As previously underlined by Guerra & Ederra (2015), from *Fissidens rivularis* three main differentiating characters can be emphasized: autoecy (*F. rivularis*) vs. dioecy or synoecy (*F. jansenii*); acute-mucronate apex and nerve confluent with limbidia (*F. rivularis*) vs. bluntly acute apex and limbidia not reaching nerve (*F. jansenii*); absence of bistratose lamina, except for the occurrence of paracostal patches (*F. rivularis*) vs. frequent occurrence of laminal bistratose spots (*F. jansenii*). It should be noted however that the nerve may on occasion form a mucro in perichaetial leaves in *F. jansenii*. In the field, *F. rivularis* is a larger plant with slightly wider leaves compared to *F. jansenii*.

Distribution of sex organs is widely variable in both species, synoicous forms have rarely been reported in *Fissidens rivularis* (Sérgio & Pursell 2001) although they have not been detected in French populations. The occurrence of strictly terminal antheridial bundles is restricted to *F. jansenii* and appears to afford a good taxonomic character. The occurrence of differentiated very narrow perichaetial leaves (at least two times narrower than lower leaves) have not been observed in *F. jansenii* (where perichaetial leaves are of the same width than lower leaves).

The morphological proximity of *Fissidens jansenii* and *F. rufulus* has not been previously discussed in Sérgio & Pursell (2001). Both species share an aquatic habitat and a similar growth form, show similar leaf apex characters combining small cell size and frequent synoiecy (Bruggeman-Nannenga 1982). However, *F. rufulus* has shorter and wider proximal leaves (Table 1), and the limbidia are clearly more robust (wider and thicker) in *F. jansenii* than in *F. rufulus*. In *F. rufulus* the apex is never mucronate whereas in *F. jansenii* it is occasionally the case. In the field, the most useful distinction is the form of the leaves (compare leaves of same position along stem, preferably apical ones); they are long and narrow in *F. jansenii* vs. shorter and wider in *F. rufulus*. Genetic study of this taxa complex is needed to clarify the phylogenetic position of *F. jansenii*.

Fissidens jansenii shares with *F. rivularis* and *F. rufulus* a similar habitat. They are obligate aquatics, but are more precisely described as amphibious taxa, sharing a two-phase biological cycle: they are submerged during winter months or during occasional flow episodes, and are exposed when the water level drops. Their precise ecology needs to be studied, but *F. rufulus* is apparently restricted to fast-flowing limestone or sandstone watercourses (Dierssen 2001) and is only occasionally found on acidic rocks (Erzberger

Table 1. Main differentiating characters of *Fissidens jansenii*, *F. rivularis* and *F. rufulus* (characters of *F. jansenii* are based on new French populations reported herein, those of the two other species from our experience of French populations).

	Fissidens jansenii	***Fissidens rivularis***	***Fissidens rufulus***
Size of the shoot (cm)	0.2–1.2	0.5–2	1–3.5
Form of vegetative leaves	Oblong-lanceolate to narrowly lanceolate	Narrowly lanceolate	Lanceolate to oblong-lanceolate
Ratio L/w (of vegetative leaves)	5.6–8.1	3.5–8	2.5–4.5
Limbidium at apex	Limbidium mostly not reaching apex	Limbidium reaching apex	Limbidium not reaching apex
Form of apex	In proximal leaves acuminate with limbidium not reaching apex (border at more than 50 µm long from apex); in distal leaves limbidium not reaching apex, but forming a mucro or occasionnaly reaching apex and forming a stout mucro	Mucronate	Limbidium never reaching apex, neither in proximal or distal leaves (more than 90 µm distant from apex)
Nerve excurrency	No or distincly mucronate only in distal leaves	Yes (in all leaves)	No
Stratification of vegetative leaves	Bistratose patches in vaginant and dorsal lamina	Unistratose	Unistratose
Width of the limbidium in the dorsal lamina (µm)	18–22	20–30	12–19
Stratification of dorsal limbidium	3 to 5	2 to 4	2 to 3
Occurrence of intralaminar limbidium	No	No	Yes
Median cells size (µm)	8–12 × 6–9	6–9 × 6–9	6–10 × 5–10
Sexuality	Dioicous or sinoicous	Autoicous	Dioicous or sinoicous
Spore diameter (µm)	12–17	15–20	25–35

2016) where it may be influenced by calcareous content of the water (Blockeel et al. 2014). In France however it is also found on strongly acidic bedrock with a low mineral content (pers. obs.). On the contrary, *F. rivularis* is more strictly associated with acidic water although rarely it has been reported on limestone (Blockeel et al. 2014).

Hitherto, *Fissidens jansenii* was only known from the type locality in Portugal. The 10 new localities in France, all located on the Plateau de Millevaches, represent a significant northward extension of the geographical range of *F. jansenii*. Provisionally it could be considered a Suboceanic-temperate species. Judging from the number of localities, it is likely to be a long established member of the French bryoflora. Further survey is needed to gain a better understanding of the seemingly disjunct geographical distribution and it should be searched for in north-western France and the British Isles where many suitable habitats exist. The plants can only be looked for when the water flow is very low so that targeted search should be made during low-water periods.

Conservation

Fissidens jansenii was previously known only from the waterfall at Poço do Inferno and downstream along the river, Serra de Estrella, at an altitude ca. 1100 m. It was previously thought to be a narrow endemic and considered Critically Endangered in Portugal and Europe (Sérgio et al. 2019; Hodgetts et al. 2019). Taking into consideration the new populations mentioned here this globally rare species would be evaluated as Vulnerable since it is estimated that there are fewer than 10,000 individual-equivalents in Europe, and that each subpopulation has fewer than 1,000 individual-equivalents. The current population trend is decreasing slightly. It is certainly threatened, as it is both rare and surely declining although the last cannot be precisely estimated owing to the lack of historical data.

In Portugal the main threats are linked to water (eutrophication, pollution, canalization) and vandalism (Sérgio et al. 2013). The practice of "water sports" (canoeing, canyoning) seems to be particularly worrying. An indirect threat is related with fire as the hydraulic systems can be affected by erosion and debris deposition following fire events.

On Plateau de Millevaches, the situation appears to be somewhat more favourable. The area of occupancy is far more extensive, reaching approximately 100 km². The number of populations is 10 so that it can be considered a typical floristic element of oligotrophic rivulets of this region. All populations observed are spore producing which facilitate recruitment of new sub-populations.

Nonetheless, the conservation status of *Fissidens jansenii* is undoubtedly of concern in France. The populations are invariably small, comprising several tiny patches at one locality. The most serious threat is the deterioration of the water quality of the rivulets. Plateau de Millevaches is a livestock (mainly cattle and sheep) farming area and in many instances signs of habitat degradation are apparent: severe trampling of riversides, cows

fouling the water, seepage of agricultural pollutants, Riprap technique used to stabilize eroding streambanks, etc.

The typical watercourses hosting populations of *Fissidens jansenii* occur in a vast peatland of a river basin head which is in turn threatened by intensive agricultural practices (fertilizer application and physical disturbance) and this may constitute an aggravating factor.

Another serious threat is the damming of rivers for hydroelectricity. *Fissidens jansenii* is clearly linked to small dynamic hydrosystems, where freshly exposed bare surfaces are created by scouring and flooding from place to place.

Acknowledgments

Thierry Vergne provided the map. Cecilia Sérgio is thanked for sending isotype of *Fissidens jansenii*. Ida Bruggeman-Nannenga and Ron Porley kindly examined specimens collected in France. Ron Porley also offered many suggestions to improve an early version of this text. César Garcia provided details about the conservation status of *F. jansenii* in Portugal.

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Manuscript received: August 20, 2019
Accepted: October 9, 2019
Responsible editor: J.A. Jiménez Fernández