

A taxonomic conundrum resolved: the transfer of *Grimmia horrida* to *Coscinodon* based on sporophyte discovery in France, with support from molecular data

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ABSTRACT. *Coscinodon horridus*, formerly *Grimmia horrida*, is reported as new to France from two localities. Sporophytes are described for the first time. Morphological and molecular evidence are presented supporting the transfer of *G. horrida* to *Coscinodon*. The variability of the species and reproductive traits are discussed and it is compared with morphologically similar taxa.

KEYWORDS. Hair-point, European moss endemic, France.



Grimmia horrida J. Muñoz & H. Hespanhol was described recently from the northwest Iberian Peninsula (Muñoz et al. 2009) and it is therefore not included in recent world checklists of the genus *Grimmia* (Greven 1995, 2003; Muñoz & Pando 2000) and Maier (2010). This species is most easily distinguished from other *Grimmia* species by the conspicuously ciliate hair-point. Muñoz et al. (2009) suggested that *G. horrida* belongs to the subgenus *Orthogrimmia* Schimp. based on the plane leaf margins and keeled leaves (see Hernández-Maqueda et al. 2008). In the course of recent bryological surveys in southeastern France, one of us (VH) collected a single cushion of a capsule-bearing *Grimmia* with strongly spinulose hair-points. Microscopical examination of the material suggested that the plant may be *G. horrida*, and subsequent examination of the holotype of *G. horrida* supported this view. Gametophytic material was sent to RDP who confirmed that it was indistinguishable from Portuguese specimens of the species *G. horrida*. One sporophyte bearing a large campanulate plicate calyptra was observed in French material. Since this character points towards a greater affinity to *Coscinodon*, the generic placement of *G. horrida*

needed to be addressed. At that time, RDP was collaborating with MSI (and others) on *Coscinodon monchiquensis*, a new species from the Serra de Monchique in the Algarve province, Portugal (Ignatov et al. 2018), and thus the opportunity of including the French material in the DNA analysis of *Coscinodon* was taken.

Following the initial discovery of a colony, a targeted search located a second and larger French population of *Grimmia horrida*, also with sporophytes. *Grimmia horrida* was initially described from sterile material, and therefore we describe and illustrate the sporophyte for the first time in this paper. Additionally, a full description of gametophyte features is provided and it is compared with morphologically similar taxa.

MATERIAL AND METHODS

Molecular data. The nuclear ITS region was found to be so far the only molecular marker useful for the phylogenetic study of *Coscinodon* at the species level (Ignatova et al. 2008; Ignatov et al. 2018). It was thus used in the present study, including most of the molecular data sets from these previous studies, with three additional specimens of *Grimmia horrida* (**Table 1**). Outgroup taxa were selected after certain attempts to align *Coscinodon* data with a number of *Grimmia* species. This

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Table 1. Newly sequenced specimens from this study.

| Species (as in Fig. 1) | Voucher | GenBank accession number |
|------------------------------|---|--------------------------|
| <i>Coscinodon horridus</i> 1 | France, Montusclat, La Tortue, Haute-Loire, Huggonot, 20 February 2017 (MHA) | MH364378 |
| <i>Coscinodon horridus</i> 2 | Portugal, Serra do Marão, Covelos, Trás-os-Montes, Porley, 21 August 2011 (MHA) | MH364379 |
| <i>Coscinodon horridus</i> 3 | Portugal, Serra da Peneda, Ameijoeria, Minho, Porley, 27 August 2013 (MHA) | MH364380 |

was not easy, as the ITS of different *Grimmia* species are exceedingly difficult to align. The included species were found to be maximally similar and alignable to *Coscinodon* by ITS. Their close position to *Coscinodon* was found also by Hernandez-Maqueda et al. (2008) using other gene regions. *Grimmia mollis* was used for tree rooting in MP analysis, as it was the least similar among outgroup taxa.

DNA extraction and amplification followed common laboratory protocols described by Gardiner et al. (2005). Data on newly obtained sequences are given in **Table 1**. Sequences were aligned in Bioedit (Hall 1999) by the built-in ClustalW option (Thompson et al. 1994), with subsequent manual edition. Aligned sequences (844 positions, **Supplementary Table S1**) were complemented by coded indels, and an indel of any length was coded manually (C deletion, T insertion) as a single mutational event (90 positions), and incorporated into the end of the alignment (**Supplementary Table S2**). Bayesian analyses were conducted following a Bayesian Markov Chain Monte Carlo approach using MrBayes v.3.1.2 (Ronquist & Huelsenbeck 2003). The three partitions (ITS1, 5.8S RNA, ITS2) were analyzed with the GTR+G model as selected by MrModeltest2.3 (Nylander 2004), and the indel partition was analyzed using the restriction site (binary) model. Three parallel runs were implemented, each with five chains and 40,000,000 generations, with trees sampled every 1000 generations. Burnin was set to exclude 10,000,000 generations. The chain temperature was set at 0.015 in all analyses. The stationary phases of analyses were tested by sump for the absence of differences in distribution of LnL since 25% burn-in, by reaching for all parameter RSRF 1.000 and ESS exceeding 200 in Tracer1.6 (Rambaut et al. 2014). In addition, maximum parsimony analysis was completed with Nona (Goloboff 1994) within the Winclada shell (Nixon 1999), using the same alignment with indel coding data (**Supplementary Table S2**), with a bootstrap calculation with 2000 replications (Pa-

rameter: number of search reps 10, starting tree per rep 10, max tree 100, do max*, Save consensus).

Morphological data. Morphological examination was carried out using conventional microscopical methods. The illustrations and the morphological description are based on French Haute-Loire specimens. The holotype of *Grimmia horrida*, housed in MA (MA 37866, Madrid), was examined and compared with the French plants, as were specimens from Portugal (Serra do Marão, Covelos, Trás-os-Montes, 21 August 2011, R. D. Porley). Specimens of *Coscinodon cribrosus* from Massif Central, France, were also examined for comparison. Details of localities for *C. cribrosus* are available upon request from the first author.

RESULTS AND DISCUSSION

Phylogenetic results. Molecular phylogenetic analyses by both maximum parsimony and Bayesian approaches resulted in trees with a similar topology; thus we only discuss hereafter the Bayesian tree, which was slightly better resolved. The bootstrap support values from the maximum parsimony analysis are, however, added to the Bayesian tree shown in **Fig. 1** for completeness.

Being rooted at *Grimmia mollis*, three species of *Grimmia* (*G. reflexidens*, *G. caespiticia* and *G. montana*) formed a basal clade (PP=0.88, BS<50). Another clade was formed by two specimens of *G. trinervis* (PP=1.0, BS=100), while a maximally supported clade (PP=1.0, BS=100) included all of the representatives of the genus *Coscinodon*, including *G. horrida*. Specimens of *G. horrida* formed a clade with low support (PP=0.72, BS=51), which was resolved as sister to the *C. monchiquensis* clade (PP=0.99, BS=94), and their combined clade was sister to all other *Coscinodon* species. The *C. monchiquensis* and *G. horrida* clade achieved relatively high support only in parsimonious analysis (BS=89), while Bayesian posterior probability was very low (PP=0.58). The support for the clade of other species of *Coscinodon* has otherwise higher support in Bayesian analysis (PP=0.98, BS=51), and

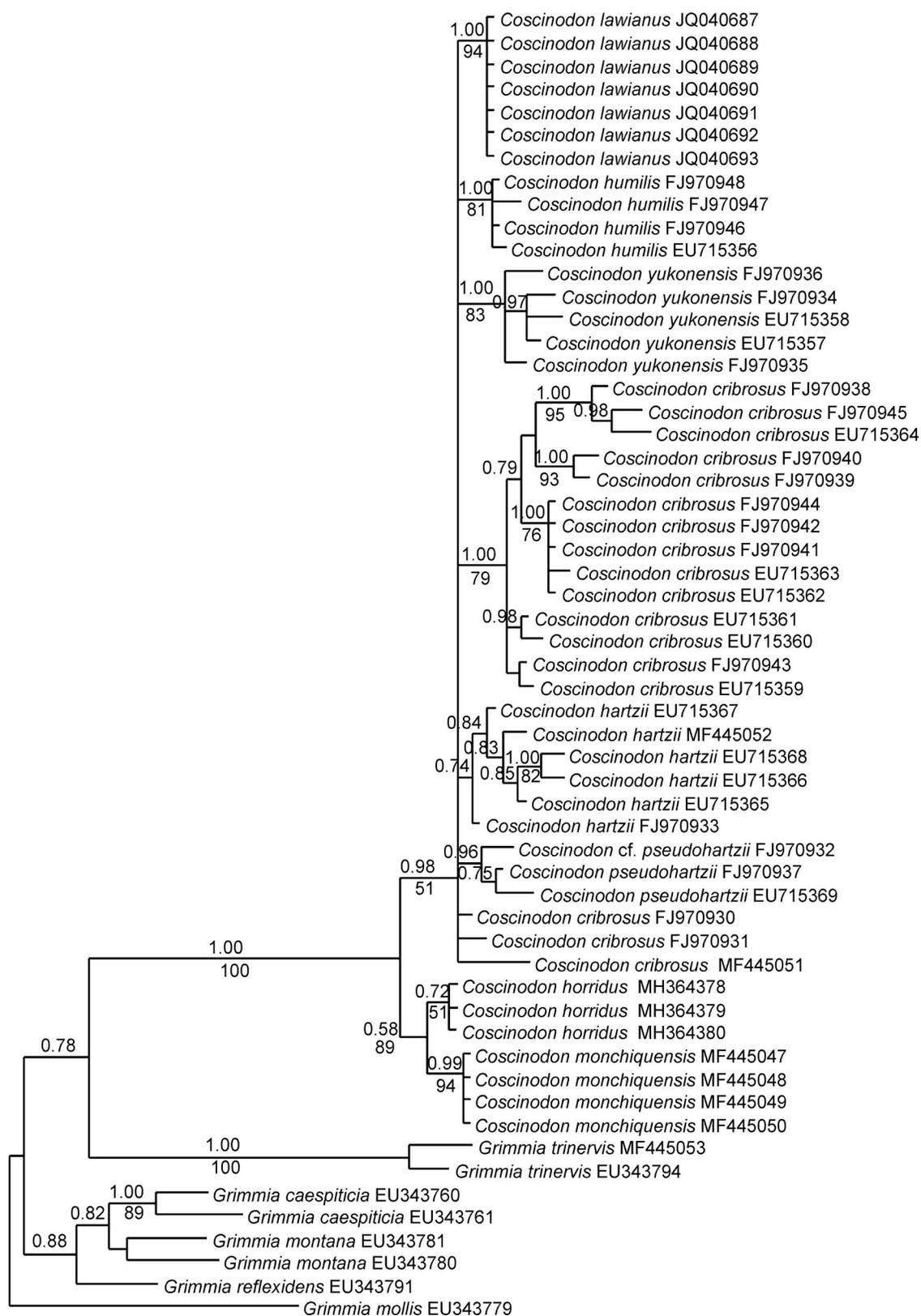


Figure 1. Bayesian tree of *Coscinodon*. Bayesian posterior probabilities (>0.50) are shown above branches, and bootstrap supports (>50) from maximum parsimony analysis are shown below branches.

most individual species within it were resolved with high support (Fig. 1). From the alignment itself, the dissimilarity of *Grimmia horrida* and *Coscinodon monchiquensis* from all other *Coscinodon* species includes three substitutions and one expanded deletion of ca. 50 nucleotides (the only case of long deletions in *Coscinodon* ITS). However, the difference between *G. horrida* and *C. monchiquensis* includes only one substitution (in which *C. monchiquensis* is unique among the studied species) and also three indels, mostly not unique, which explains why *G. horrida* obtained only a very low support.

Evidence for the transfer of *Grimmia horrida* to *Coscinodon*. Although our study is aimed at resolving the affinity of only one puzzling species, and consequently, it does not address generic issues in the family, it is important to emphasize that Ignatov et al. (2018) previously discussed why rejection of paraphyletic *Coscinodon* and its merger into a wide-encompassing genus *Grimmia* is undesirable. The genus *Coscinodon* undoubtedly forms a natural group from both morphological and ecological standpoints. If the view that only monophyletic taxa are taxonomically acceptable is rigidly adhered to, then it would logically follow, for example, that *Schistidium* Bruch & Schimp. would be included in *Grimmia*. This would not only lead to profound nomenclatural implications, but it would also become an unwieldy genus.

As already noted, Muñoz et al. (2009) postulated that *Grimmia horrida* belongs to subgenus *Orthogrimmia* Schimp. on account of the plane leaf margins and keeled leaves. The phylogenetic reconstructions provided herein, including a broad selection of other *Coscinodon* species, indeed indicates their origin from an orthogrimmian ancestor. *Grimmia horrida* has in common the following characters with species of the genus *Coscinodon*: (i) an emergent sporophyte; (ii) a campanulate plicate calyptra (Fig. 3), which covers the capsule below the middle, but totally when the capsule is young (in *Grimmia* the calyptra is mitrate or cucullate and very small, barely covering the operculum); and (iv) fenestrated peristome teeth. Vegetative characters are more ambivalent and do not unequivocally allow for a placement in *Coscinodon*. The greyish to a somewhat glaucous plant color of young leaves of *G. horrida* is reminiscent of *C. cribrosus* (Hedw.) Spruce, but this characteristic is by no means restricted to *Coscinodon* since it also occurs in several species of *Grimmia*.



Figure 2. A. Habitat of *Coscinodon horridus* (J.Muñoz & H.Hespanhol) Hugonnot, R.D.Porley & Ignatov. B. Colony of *Coscinodon horridus* showing two morphs of the same species.

Therefore, we propose to transfer *G. horrida* to the genus *Coscinodon*, and accordingly a new combination is required.

Details of the French collections. France, Haute-Loire, Queyrières, Forêt domaniale du Meygal, Le Testavoire, 1410 m a.s.l., 20 July 2015, coll. Vincent Hugonnot, s.n. (private herbarium VH; RDP); Haute-Loire, Montusclat, la Tortue, 1250-1300 m a.s.l., 20 February 2017, coll. Vincent Hugonnot, s.n. (private herbaria of VH; PC; CLF; MHA).

TAXONOMY

Coscinodon horridus (J.Muñoz & H.Hespanhol) Hugonnot, R.D.Porley & Ignatov, *comb. nov.*

Figs. 2B & 3

≡ *Grimmia horrida* J.Muñoz & H.Hespanhol, *The Bryologist* 112:326. 2009. TYPE: PORTUGAL. TRÁS-OS-MONTES E ALTO DOURO: Serra do Marão, Seixinhos, 29TNF9363, 1236 m, 3 July 2005, H. Hespanhol, s.n. (holotype, MA 37866!; isotypes: PO 4991[n.v.], LISU 225895[n.v.]).

Description of the French specimens. Plants small, in short dense cushions, 1–2 cm diameter, blackish-olive green, occasionally with a greyish or glaucous tinge, and appearing hoary due to the long hyaline hair-points. Stem short, 0.5–1 (–1.5) cm tall, simple or sparsely branched, with smooth brownish rhizoids at base; in transverse section indistinctly 5-

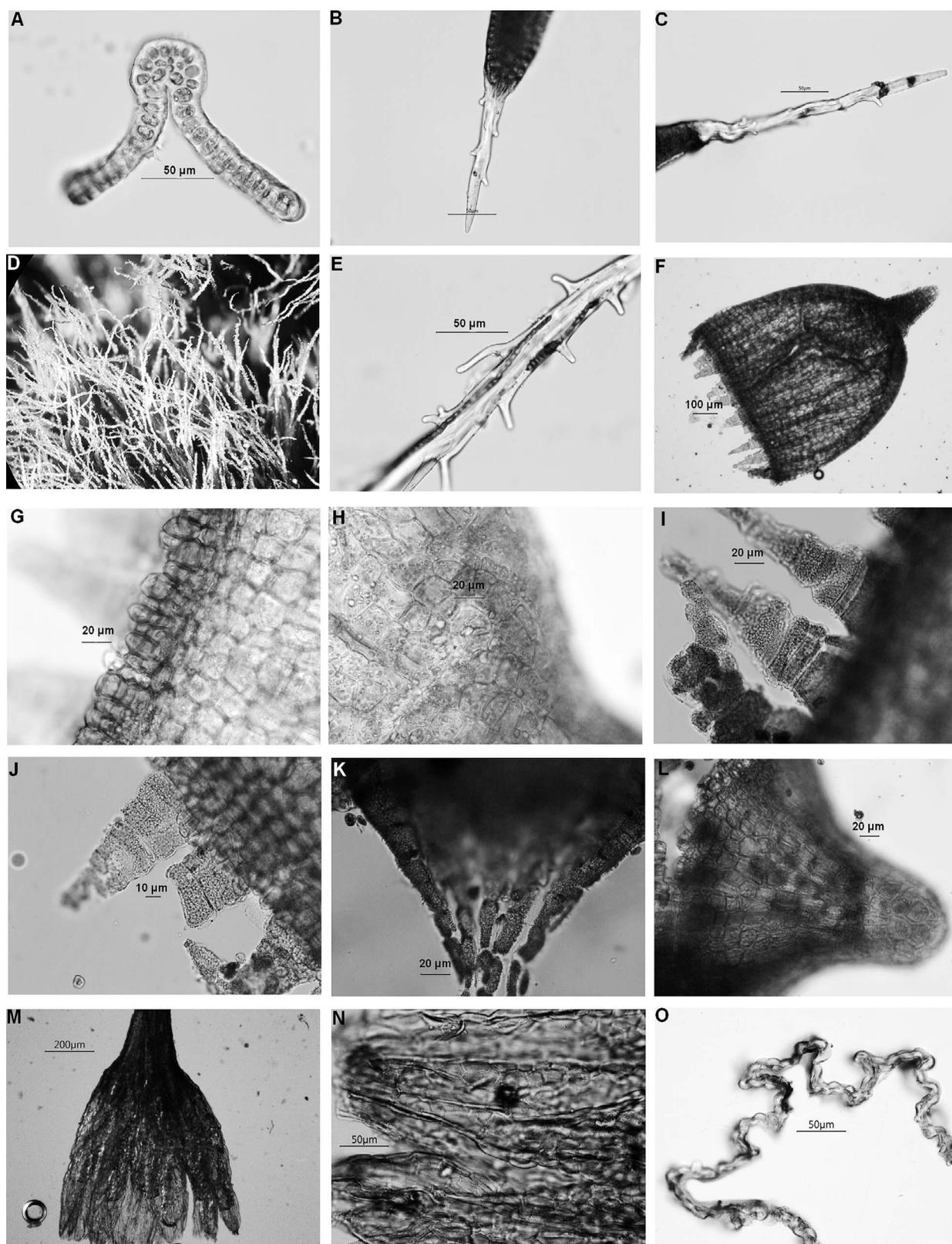


Figure 3. *Coscinodon horridus* (J.Muñoz & H.Hespanhol) Hugonnot, R.D.Porley & Ignatov. **A.** Transverse section through leaf. **B & C.** Hair-point of lower leaves. **D & E.** Hair-point of upper leaf. **F.** Urn. **G.** Annulus. **H.** Stomata. **I & J.** Peristome, outer side. **K.** Peristome, inner side. **L.** Operculum. **M.** Calyptra. **N.** Plicae of calyptrae, surface view. **O.** Transverse section through calyptra.

angled, composed of a 1–2 layered cortex of small and thickened cells and a central strand of several thin-walled collapsed cells. Lower leaves scale-like and mucous, progressively or abruptly larger and better differentiated ascending the stem. Upper leaves erect-patent when moist, scarcely altered when dry, margins plane throughout, oblong-lanceolate, sometimes with expanded base, spirally inserted on stem although appearing in 3 indistinct ranks, carinate in distal portion (keel formed by the dorsally protruding costa and spreading blades of lamina), concave proximally, 1.3–1.7 mm long (excluding hair-point) \times 0.25–0.35 μm wide, terminating abruptly in a long hair-point, terete at base, up to 0.8–1 mm long, strongly spinulose-ciliate, with cilia up to 50 μm long, some reflexed or inflexed, with distal part parallel to the hair-point. Laminal median cells rectangular, with yellowish weakly sinuose thickened walls, 10–25 μm long \times 8–12 μm wide; apical cells shortly rectangular, quadrate-isodiametric to oblate, 8–10 μm wide; basal marginal cells in lower leaves rectangular with thickened transverse walls, in upper leaves forming a hyaline marginal band of rectangular to elongate thin-walled cells; basal paracostal cells rectangular with thickened nodulose walls, or weakly so. Lamina unistratose at base, bistratose at margin for some rows distally and entirely bistratose at apex. Costa 40–50 μm wide at the base, channeled ventrally, strongly demarcated from the laminal cells, transverse section at insertion with 4 enlarged ventral guide cells, with adaxial walls strongly thickened, and a weakly developed hydroid strand of 2–3 cells; in laminal part with 2 enlarged ventral cells recessed in deep furrow; apical part composed of nearly homogeneous cells constituting a channeled, or more rarely semi-terete apex.

Apparently dioicous, perigonia not seen. Perichaetial leaves similar to but larger than vegetative leaves, rarely with margins indistinctly recurved on one or two sides, and areolation laxer at base; hair-point long and ciliate; archegonia brownish, up to 50 μm long; paraphyses uniseriate to 225 μm long. Seta straight or slightly curved, 580 μm long; seta cells quadrate to shortly rectangular, 12–22 μm long \times 8–15 μm wide, weakly dextrorse in upper part. Capsule immersed, smooth, ovoid-oblong, 0.95 mm long \times 0.36 mm wide, symmetric, wide-mouthed; operculum conical with a short, blunt straight apiculus; exothecial cells irregularly rectangular, more rarely quadrate or hexagonal, 24–50 μm long \times 10–25 μm

wide, becoming quadrate to transversely rectangular at the mouth, with thin walls; 2–3 stomata at capsule base, 28 μm diameter, concolorous with exothecial cells. Peristome teeth persistent but rather fragile, open when dry (xerocastique), 16, erect, yellowish, triangular-lanceolate, with subulate apex, 120–180 μm \times 45–55 μm at base, with irregular margins, perforate longitudinally or not, sometimes with a small filiform appendage on one side, as if tooth is deeply and asymmetrically cleft; fine trabeculae on the outer surface; teeth deeply inserted (3–5 cells) below mouth, papillose-verrucose throughout on both surfaces. Vaginula with remnants of several archegonia, 420 μm long \times 230 μm wide. Annulus of 3–4 rows of transversely oblong to rounded, incrassate cells, fragmenting irregularly. Spores mostly immature, some apparently mature, spherical, 7–9 μm in diameter, smooth. Calyptra campanulate, plicate, 5–7 lobed at base, 1 mm long \times 0.52 mm wide, covering most of the immature capsule.

Reproduction. *Coscinodon horridus* was originally described from sterile material and was assumed to be dioicous since sporophytes or gametangia were not found in the numerous collections (Muñoz et al. 2009). However, Porley (2012) mentioned archegonia-bearing individuals from Portuguese collections. In the two French populations, archegonia are very frequent. Out of almost one hundred cushions examined, approximately 95% appeared to have archegonia. Sporophytes are rare as only 13 cushions bearing capsules were seen with no more than five sporophytes in each. Perigonia were not seen despite intensive search, supporting the view that *C. horridus* is dioicous. Male plants of dioicous *Grimmia* often grow in separate cushions at some distance from female plants (Greven 2003). Male cushions of *G. montana* were seen on several occasions in mixed stands with female *C. horridus* but no sporophyte-bearing plants of *C. horridus* were detected in such stands. Furthermore, the molecular data gives no suggestion of hybridization. At the time of collection, most of the spores in the French material were immature but it is likely that in France at least *C. horridus* reproduces sexually and viable spores are produced. A monitoring of reproductive cushions will be undertaken in the future. Flagelliform fragile shoots with proximal rhizoids and bearing much reduced mucous leaves were seen rarely, and may play a role in short-distance dispersal.

Geographical distribution. The new localities in France represent a significant extension of the known geographical range of *Coscinodon horridus* (Fig. 4). Porley (2012) mentioned the possibility of finding new populations in the Atlantic biogeographic zone. Hitherto, *C. horridus* was known from a few localities (three in northern Portugal and one in north-west Spain) in the Iberian Peninsula, although sub-populations are extensive. With the new extension of range, it could be provisionally considered a Suboceanic-Temperate species. In France, the two populations are less than one kilometer apart, but this could be an artefact due to non-detection of the species between sub-populations or alternatively may indicate a species in the early stages of spread. However, the rather high number of cushions indicates a well-established species. Interestingly, not all ecologically similar sites have populations of *C. horridus*. Several localities have been visited to search for *C. horridus* without success despite their apparently suitable habitats. Further survey is needed to gain a better understanding of the geographical distribution of the species.

Coscinodon horridus brings the total number of *Coscinodon* species currently recognized in Europe to four, including *C. cribrosus*, *C. humilis* Milde and the recently described *C. monchiquensis* R.D.Porley, Ochyra & Ignatova. Furthermore, both *C. horridus* and *C. monchiquensis* are presently known only in Europe.

Ecology. The ecological conditions of the French localities seem to have much in common with those on the Iberian Peninsula except that the climate is much less oceanic. The climate of the French region where the species occurs is continental montane, influenced by the nearby Cévennes mountain range. Winters are cold, prolonged and snowy. Precipitation varies from 1050 to 1100 mm per year (Darnis 2001).

At Forêt domaniale du Meygal, Le Testavoire, in the south-east Auvergne region of France, two small cushions of *Coscinodon horridus* were found at a moderately high altitude (1410 m), on a large insolated rock that is part of a vast phonolithic (a lava which generally supports an acidic bryoflora) boulder consisting of large blocks (from 50 cm to several meters in diameter) (Fig. 2A). *Picea abies* (L.) H.Karst. plantations or natural *Pinus sylvestris* L. woodlands on acid soils are found in the surround-

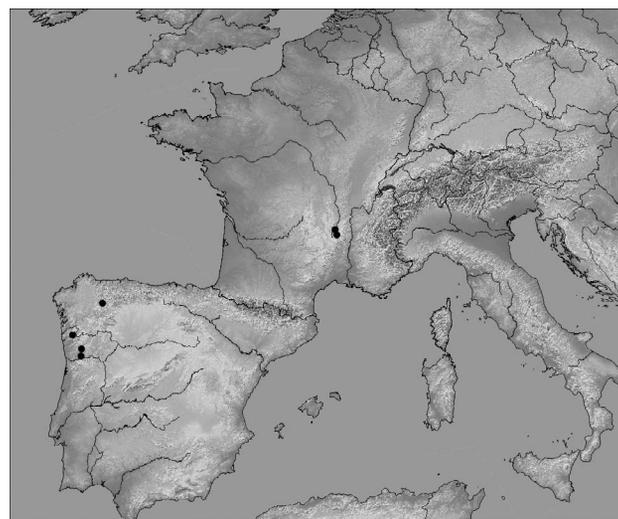


Figure 4. Known global distribution of *Coscinodon horridus* (J.Muñoz & H.Hespanhol) Hugonnot, R.D.Porley & Ignatov.

ings. On the outcrop vascular plants are scarce; scattered individuals of *Cryptogramma crispa* (L.) R.Br. ex Hook., *Valeriana tripteris* L., *Avenella flexuosa* (L.) Parl. were encountered from place to place. The bryophyte community was more diverse. *Polytrichum juniperinum* Hedw., *Ceratodon purpureus* (Hedw.) Brid., *Pohlia nutans* (Hedw.) Lindb., *Bryum argenteum* Hedw. occur on horizontal surfaces where substantial amounts of organic detritus accumulate. Bare rock is colonized by numerous cushions of *Grimmia* species, including *G. donniana* Sm. and *G. muehlenbeckii* Schimp. *Grimmia incurva* Schwägr. occurs preferentially in sheltered niches along with *Barbilophozia hatcheri* (A.Evans) Loeske. *Grimmia montana* Bruch & Schimp. is present but rare. *Andreaea heinemannii* Hampe & Müll. Hal. is also abundant on large blocks at the summit.

Montusclat, la Tortue, the second locality where *Coscinodon horridus* occurs, is of lower altitude (1250–1300 m) but supports more than 800 cushions. The area of occupancy of the population is 24,000 m². The habitat is similar to that described above. Associated bryophytes are mostly *Grimmia montana*, *G. donniana*, *G. incurva*, *Andreaea rupestris* Hedw., *A. heinemannii* and occasionally *G. laevigata* (Brid.) Brid. *Coscinodon horridus* grows either on large exposed blocks or in sheltered niches. On insolated stands, it forms small compact, blackish tufts with some stems bearing long ciliate hair-points while other stems bear only shorter and less ciliate ones. Individuals growing in shade are more robust,

deep-green, and bear only long and ciliate hair-point at the apex of the stems.

Taxonomic differentiation. *Coscinodon horridus* is a distinct species, unlikely to be mistaken for any other moss in the European flora. The hair-points are characteristically long and hyaline and are adorned with long cilia, which are bent to various angles, a unique feature of this species. Only hair-points on the upper leaves and perichaetial leaves clearly show this morphology. The lower leaves are characterized by shorter hair-points, which are sometimes only weakly ciliate or dentate. The number, size and inclination of cilia are rather variable; some specimens have very long reflexed or inflexed cilia, whereas others are smaller and faintly curved.

Gametophytes of *Coscinodon horridus* are to some degree similar to both *Grimmia montana* and *G. incurva*, as highlighted in Muñoz et al. (2009) and Porley (2012). From *G. montana* it differs in the keeled apex with spreading lamina, while the former has a dorsally smooth upper leaf with increasingly incurved leaf margins. The upper lamina of *G. montana* in transverse section is predominately bistratose, whereas in *C. horridus* the lamina is bistratose only in the apex and the upper leaf margins, and furthermore *G. montana* has quadrate to short-rectangular basal cells as opposed to elongate basal cells in *C. horridus*. *Grimmia incurva* differs by the incurved subulate leaves when dry, and in the middle part of the lamina the dorsal costal cells are markedly longer than the adjacent laminal cells; in *C. horridus* they are of more or less equal length.

Extensive mixed stands were studied in the field and revealed several subtle but constant features allowing field, or at least stereomicroscope, differentiation of material. *Grimmia incurva* does not pose many difficulties since the color is at once distinct; it is often brownish (or has a brownish tinge in at least apical part of the leaves) and smaller forms exhibit short hair-points or lacking, whereas *Coscinodon horridus* is greenish and even the smallest forms have a long and ciliate hair-point. *Grimmia incurva* has several leaves incurved (imparting a crispate appearance to the tuft), whereas they are straight in *C. horridus*.

Conversely, *Grimmia montana* is more difficult to separate in the field. In mixed tufts, *Coscinodon horridus* is almost always smaller than *G. montana*

and vegetatively less vigorous. However, *G. montana* has at most a bluntly denticulate hair-point. Upon wetting, the habits of the female colonies of the two are distinct: the leaves of *C. horridus* are straight, stiff, and imbricate whereas those of *G. montana* are laxer and sigmoid. This morphological characteristic is precisely illustrated photographically by Greven (http://www.grimmiasoftheworld.com/gallery/Grimmia_montana_var_horrida/#5). The apical part of the lamina is markedly concave in *G. montana* with incurved margins, whereas it is spreading from the nerve in *C. horridus* and is less concave, rarely almost plane with the nerve protruding dorsally.

From other species of the genus *Coscinodon*, *C. horridus* is uniquely differentiated by the ciliate hair-point. From *C. cribrosus* it differs further in having linear foliar apices (vs. triangular), non-plicate leaves (vs. normally plicate, often with longitudinally bi- to tristratose bands, resembling “secondary costae,” although plicae maybe weakly developed in some populations), non-membranous perichaetial hair-point (vs. wide-membranous perichaetial hair-point, and less strongly cribrose peristome teeth).

The absence of leaf plicae in *Coscinodon horridus* is shared by the closely related *C. monchiquensis*. *Coscinodon monchiquensis* and *C. horridus* are two examples of species exhibiting a *Grimmia*-type gametophyte but with a *Coscinodon*-type sporophyte. *Coscinodon horridus* is immediately distinguished by the hair-point (ciliate in *C. horridus* and smooth to bluntly denticulate in *C. monchiquensis*). Other important differences include stratification of the distal lamina (unistratose to partially bistratose in *C. horridus* vs. wholly bistratose in *C. monchiquensis*) and a recurved basal leaf margin in *C. monchiquensis*, an unusual character state in *Coscinodon* (plane in *C. horridus*).

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Supplementary documents online:

Supplementary Table S1. Aligned sequences (844 positions with no coded indels added) used in the placement of *Coscinodon horridus* in the genus *Coscinodon*.

Supplementary Table S2. Aligned sequences used in the study, complemented by coded indels where an indel of any length was coded manually (C deletion, T insertion) as a single mutational event (90 positions), and incorporated into the end of the alignment.

Queries for bryo-121-04-11

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