

ARTICLE

***Macromitrium nelliampathy anum* sp. nov. (Orthotrichaceae: Bryopsida),
a new moss species from the Western Ghats of India**

Macromitrium nelliampathy anum sp. nov. (Orthotrichaceae: Bryopsida),
una nueva especie de musgo de los Ghats occidentales de la India

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Abstract: During bryological work in the Nelliampathy hills (Western Ghats, India), we collected an epiphytic *Macromitrium* with unistratose leaves in which cells in the distal 1/3 of the leaf are bulging but neither tuberculate nor papillose. The specimen did not fit morphologically with any other species of the genus worldwide. We performed a phylogenetic analysis based on *trnL*-F sequence data, and compared the morphology of this specimen with the related species of *Macromitrium*. Morphological and molecular evidence support the establishment of a new species of *Macromitrium*, *M. nelliampathy anum* Sajitha, Manju & J. Muñoz, which is described and illustrated. The new species can be distinguished from all congeners by the combination of the following morphological characters: (1) branch leaves strongly curled and flexuous along its costa when dry, unistratose, (2) cells in the distal 1/3 of the leaf bulging, with smooth walls, neither papillose distally nor tuberculate proximally, (3) a very small area at the juxtacostal extreme base of cells hyaline and larger, similar to the ‘cancellina’ in calymperoid mosses, (4) basal margins with a long, single row of 12–13 hyaline cells; (5) pleated calyptra covering ¾ of the globose capsule, with a few hairs at the beak, (6) peristome teeth reduced, consisting only of a low irregular papillose outgrowth, or absent, and (7) anisospory.

Keywords: Epiphytic, Kerala, Nelliampathy hills, phylogenetic analysis, taxonomy.

Resumen: Durante una campaña briológica llevada a cabo en las colinas Nelliampathy (Ghats occidentales, India), se recolectó un *Macromitrium* epífita con hojas uniestratificadas y células del tercio distal de las hojas abombadas, pero sin tubérculos ni papilas, que no se ajustaba morfológicamente a ninguna especie del género. El análisis filogenético basado en secuencias *trnL*-F y la comparación morfológica con otras especies de *Macromitrium* respaldan el establecimiento de una nueva especie de *Macromitrium*, *M. nelliampathy anum* Sajitha, Manju & J. Muñoz, que se describe e ilustra. La nueva especie se distingue de todos sus congéneres por la combinación de los siguientes caracteres morfológicos: (1) hojas de las ramas fuertemente rizadas y flexuosas a lo largo del nervio en seco, uniestratificadas, (2) células abombadas pero con paredes lisas, sin papilas en las células distales ni tubérculos

en las proximales, (3) una zona muy pequeña en la zona yuxtacostal basal de células hialina y más grande, similar a la cancellina de Calymperaceae, (4) márgenes basales con una sola fila de 12–13 células hialinas o pelúcidas; (5) caliptra con algunos pelos en el pico, plegada, que cubre $\frac{3}{4}$ de la cápsula, que es globosa, (6) dientes del peristoma reducidos, consistentes solo en una protuberancia papilosa baja e irregular, o ausentes, y (7) anisosporia.

Palabras clave: análisis filogenómicos, epífitos, Kerala, Nelliampathy hills, taxonomía.

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Supplementary information ↓

1. INTRODUCTION

During a bryofloristic survey of the Nelliampathy Hills in the Palakkad District in the Western Ghats in India, we came across an interesting epiphytic species growing on a tree trunk, clearly belonging to *Macromitrium* Brid. (Orthotrichaceae). Our first attempt to identify the plants using all relevant treatments of Indian bryophytes (Gangulee 1977; Nair *et al.* 2005; Chaudhary *et al.* 2008; Daniels *et al.* 2018; Daniels & Kariyappa 2019; Daniels & Raja 2020; Mufeed *et al.* 2021; Sahu & Asthana 2022) was unsuccessful. The same outcome occurred when using the recently published key to Indian species of the genus (Li *et al.* 2020) or literature on the genus from neighboring areas, such as China (Guo *et al.* 2012), Papua New Guinea (Vitt *et al.* 1995), New Zealand (Vitt 1983), Australia (Vitt & Ramsay 2006), and Malesia (Fleischer 1904; Eddy 1996). Guo *et al.* (2024) recently published a world monograph on the genus, and the morphological study of our plant using this work did not yield an identification because it exhibits a combination of characters not shared by any taxon treated in this world monograph. Our specimen has branch leaves strongly curled and flexuous along the costa when dry, unistratose and with cells in the distal 1/3 of the leaf bulging, all smooth, neither papillose distally nor tuberculate proximally. The leaves have a small area at the juxtacostal extreme base where the cells are hyaline and larger, similar to the ‘cancellina’ in calymperoid mosses. Additionally, there is a long, single row of 12–13 hyaline cells at the basal margins. The pleated calyptra covers 3/4 of the capsule, the peristome teeth are absent or reduced to irregular papillose projections, and the spores are anisosporous.

Recent molecular studies have shown that *Macromitrium* is polyphyletic (Wilbraham 2022; Valente *et al.* 2023). This has led to the description of two new genera: *Aureomacromitrium* D.V. Valente, P.E.A.S. Câmara & D.F. Peralta and *Pseudomacromitrium* D.V. Valente, P.E.A.S. Câmara & D.F. Peralta to accommodate Brazilian species with pluripapillose upper cells and tuberculate basal cells, respectively (Valente *et al.* 2023). These two genera are molecularly closely related to *Groutiella* Steere, which morphologically differs from *Macromitrium* s.l. in having a short calyptra covering only the upper half of the urn and a marginal limbidium of several rows of elongated, hyaline cells (Allen 2002; Yu & Jia 2023). Most *Groutiella* species also differ from *Macromitrium* in that all basal cells are round and smooth, although in *G. tomentosa* (Hornsch.) Wijk & Margad. and *G. tuberculata* B.H. Allen & I.H. Holz they are tuberculate. In this context, the aim of this study is to establish the identity of this puzzling Indian plant considering its relationships with *Macromitrium* s.l. and *Groutiella*. Both morphological and molecular data suggest that this is an undescribed species of *Macromitrium*, here described as *Macromitrium nelliampathy anum* sp. nov.

2. MATERIAL AND METHODS

Taxon sampling and morphological study

The field work in the Nelliampathy hills (10.530° N, 76.679° E) was conducted during 2019–2024. The specimen was collected during 2022 from an old tree trunk in the grassland at the peak of the Hill Top mount (10.508° N, 76.653° E), at 1400 m a.s.l. (Fig. 1). The photographs of the specimen were taken in the field and in the laboratory. A Leica SAPO stereo zoom microscope with 12 MP Flexacam C3 microscope camera was used for morphological study and anatomical features were studied using an Olympus CX21LiLED compound microscope with Magcam DC 5.1MP, 1/2.5 CMOS sensor camera. Digital images and their measurements were taken using Magnus Analytics MagVision software (version X64.4.8.15674.2-0191008). For scanning electron microscopy (SEM) observation, dry spores and a mature sporophyte were glued to a stub and, without critical point treatment, analysed and photographed at the Scanning Electron Microscopy Department of the National Institute of Technology (NIT), Calicut, India, using a ZEISS Sigma 300 Gemini 1 scanning electron microscope at 2.00 kV. The specimens are deposited in the Calicut University Herbarium (CALI).

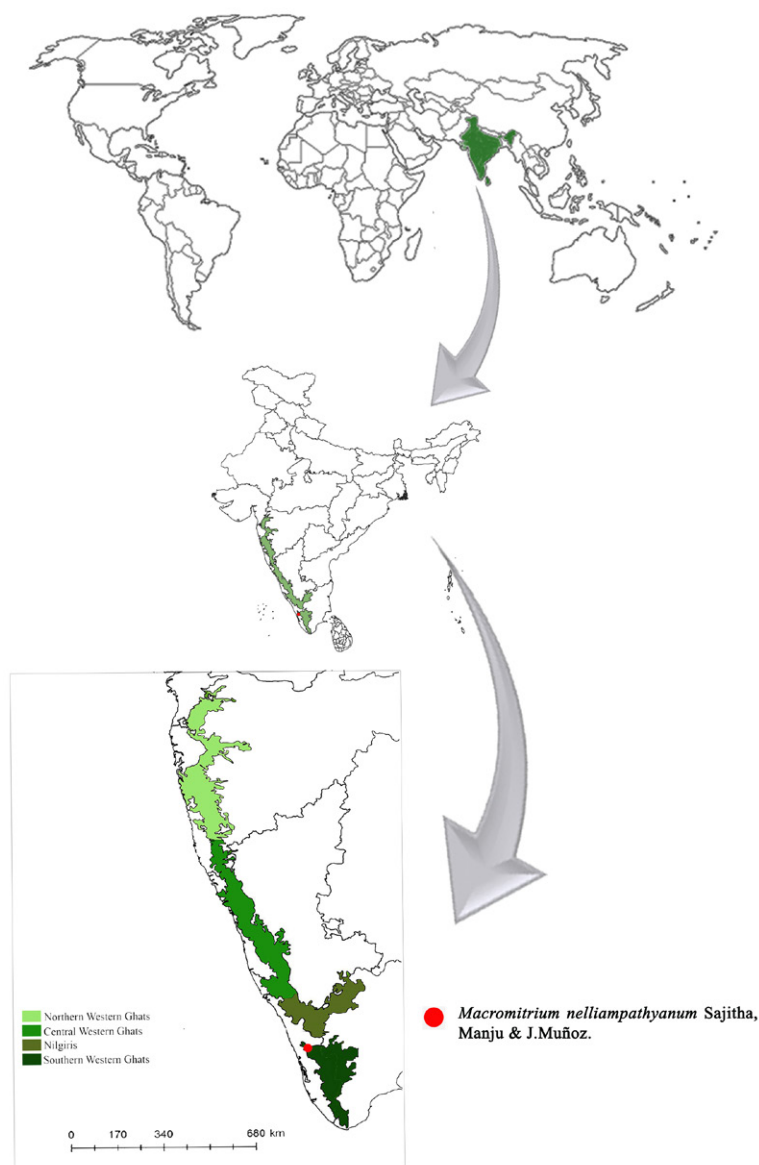


Figure 1. Distribution map of *Macromitrium nelliampathanum* Sajitha, Manju & J. Muñoz. The red circle indicates the collection site in the Western Ghats. The green patch represents the extent of the mountain systems in the western coast of India. Lines: state borders.

DNA extraction, PCR amplification and sequencing

Genomic DNA was isolated using the CTAB method (Doyle & Doyle 1987). The extraction buffer contained 100 mM Tris-HCl (pH 8), 1.5 M NaCl, 25 mM EDTA, 2.5 % CTAB (w/v), 2 % β -mercaptoethanol and 1 % polyvinylpyrrolidone. The high NaCl concentration (1.5 M) was included to remove polysaccharide contamination. Samples were incubated in extraction buffer at 55 °C for 3 h. After incubation, the lysate was extracted with chloroform:isoamyl alcohol (24:1). DNA was then precipitated using ammonium acetate and isopropanol and incubated at –20 °C for 12 h. The DNA pellet was purified with 70 % and 96 % ethanol, resuspended in 30 μ L of water purified using a Milli-Q system and stored at –80 °C.

Amplifications of the *trnL-F* region were done in 50 μ L-reactions containing 0.25 μ L DreamTaq DNA Polymerase (5 U/ μ L; Thermo Fisher Scientific, Vilnius, Lithuania), 5 μ L of 10X DreamTaq Buffer, 4 μ L of dNTPs-Mix each 2.5 mM, 4 μ L of MgCl₂ 3.5 mM, 1 μ L of each amplification primer at 10 mM (C: CGAAATCGGTAGACGCTACG and F: ATTTGAACTGGTGACACGAG; Taberlet *et al.* 1991), 33.72 μ L of distilled water and 1 μ L of template DNA. Amplification cycles were as follows: 2 min at 94 °C, followed by 30 cycles each with 2 min at 94 °C, 1 min at 55 °C, and 1 min at 72 °C, and a final 7-min extension step at 72 °C. The PCR amplicon was purified using QIAGEN QIAquick PCR Purification Kit (Cat. No. / ID: 28104). Forward and reverse DNA sequencing reaction of PCR amplicon was carried out with the amplification primers using the BDT v3.1 cycle sequencing kit on Applied Biosystems™ MiniAmp™ Plus Thermal cycler and analysed on ABI 3730xl Genetic Analyzer. All PCR products were gel purified and sequenced at C-Six labs Pvt Ltd, Kerala, India.

Phylogenetic analyses

For the newly sequenced Indian specimen, we checked the forward and reverse sequence chromatograms, generated the consensus sequence, and trimmed the primer sequences using Geneious Prime 2024.1 (<https://www.geneious.com>). This sequence was combined with the two matrices described below.

In a preliminary analysis to confirm the generic placement of the Nelliampathy plant, we downloaded all GenBank sequences of the *trnL-F* region of *Macromitrium* and *Groutiella* (Appendix 1), the most closely related genus to *Macromitrium*, and performed a Bayesian analysis with *Schlotheimia grevilleana* Mitt. as outgroup (170 sequences belonging to 42 taxa). In a subsequent analysis, in addition to the newly sequenced specimen, we used the 38 sequences of the previous matrix corresponding to the 12 species of the “*M. sulcatum*” group (Wilbraham 2022), and *Groutiella tomentosa* (Hornsch.) Wijk & Margad. as outgroup. The matrices were automatically aligned using MAFFT (Katoh & Standley 2013) in Geneious Prime with the option ‘Align full length sequences to an MSA’. This alignment was further revised manually using PhyDE 0.9971 (Müller *et al.* 2006) following alignment rules described in Kelchner (2000) and Quandt & Stech (2005). The optimal substitution model was inferred using the ModelTest-NG algorithm (Darriba *et al.* 2020) implemented in RaxMLGUI 2.0.13 software (Edler *et al.* 2021; Kozlov *et al.* 2019). Gaps were recoded as absence/presence characters using a simple indel-coding approach (Simmons & Ochoterena 2000) in PhyDE 0.9971 using the plugin SeqState (Müller 2004), treated as a single partition and added to the dataset. Both matrices and the Bayesian majority-rule consensus tree with the 170 sequences are available at the CSIC open repository (<https://doi.org/10.20350/digitalCSIC/17929>). Phylogenetic relationships were estimated using (a) RaxMLGUI 2.0.13 (Edler *et al.* 2021) with GTRGAMMA in effect and (b) Bayesian inference (BI) in MrBayes version 3.2.7a (Ronquist *et al.* 2012) employing a GTR + Γ + I substitution model for the nucleotide partitions and F81 for the indel partition. Two Metropolis coupled Markov chain Monte Carlo (MCMC), each with one cold and three heated chains, were run for 7 million generations, with a sampling frequency of 1000 generations. Stationarity of the MCMC search was evaluated in TRACER 1.7 (Rambaut *et al.* 2018) by examining the log-likelihoods and the effective sampling size (ESS), whereby ESS values > 200 were regarded as a sufficiently long run. For the extensive data set a burn-in of ~20 % (1.5 million generations) was identified, while for the reduced data set a burn-in of ~50 % (3.5 million generations) was chosen. A 50 % majority-rule tree was calculated from the remaining generations. In both cases two independent analyses were conducted: one solely based on the DNA dataset and a second including the indel matrix appended. Since the maximum likelihood and Bayesian analyses recovered the same topology, only the Bayesian tree is shown.

3. RESULTS

The length of the aligned region was 410 bp for the largest dataset and 359 bp for the “*M. sulcatum*” group dataset. Analysis of the larger data set resolved the Nelliampathy plant close to the “*M. sulcatum*” group (SF1), which was considered to be closely related to *Groutiella* by Wilbraham (2022), and has been formally recognised at generic rank as *Pseudomacromitrium* (Valente et al. 2023) to include most of the South American species formerly included in *Macromitrium*: *P. argutum* (Hampe) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta, *P. carionis* (Müll.Hal.) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta, *P. cirrosum* (Hedw.) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta, *P. guatemalense* (Müll.Hal.) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta, *P. longifolium* (Hook.) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta, *P. podocarpus* (Müll.Hal.) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta, and *P. punctatum* (Hook. & Grev.) D.V.Valente, P.E.A.S.Câmara & D.F.Peralta (SF1). The second analysis (Fig. 2), including only *Pseudomacromitrium* species, *M. blumei* Nees ex Schwägr., the Nelliampathy plant, and *Groutiella tomentosa* as outgroup, could not fully resolve their phylogenetic relationships, but based on the relationship of the Nelliampathy plant to other species, in addition to its unique morphological characters, we describe it as a new species.

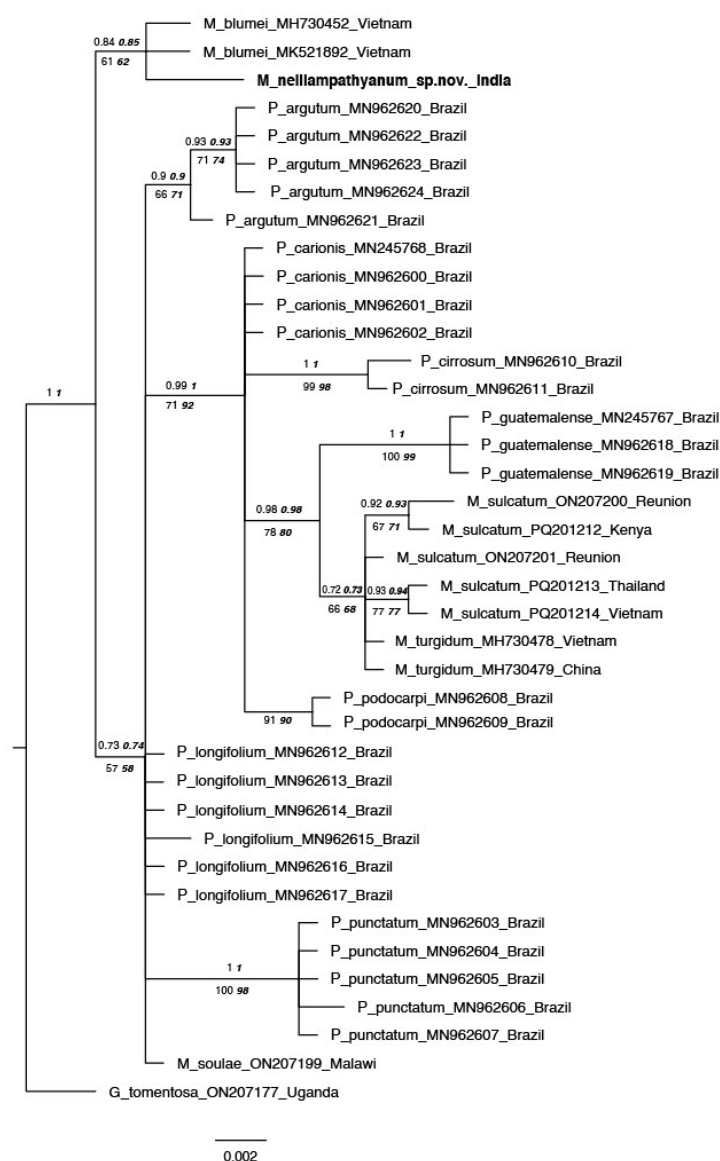


Figure 2. Bayesian majority-rule consensus tree calculated from the results of Bayesian analysis of the *trnL-F* data set of the species in the “*M. sulcatum*” group (Wilbraham, 2022). The Bayesian posterior probabilities are indicated above the branches and maximum-likelihood bootstrap values below (without indels = left, regular; with indels coded = **right, italic bold**).

Taxonomic treatment

Macromitrium nelliampathy anum Sajitha, Manju & J. Muñoz **sp. nov.** Type: India, Kerala, Palakkad District, Nelliampathy hills, Hilltop, 1400 m a.s.l., epiphytic, 3 Sep. 2022, Sajitha M.S. 194446 (holotype: CALI; isotype: CAL). **Figs. 3–6.**

Description.—Plant small, green to olive green, in glossy tufted mats; primary stems 2.5–3 cm, long creeping, covered with brownish tomentum, without a central strand. Secondary stems erect, crowded, 0.5–0.7 cm long, cortical cells 6–9.4 × 4.6–8.4 µm; medullary cells 22.7–34.8 × 13.8–20.7 µm, surrounded by a ring of thick-walled cells. Branch leaves when dry spirally twisted around the stem, strongly curled and flexuous along its costa, which obscures the spiral disposition along the branches, strongly keeled from the base to mid-leaf, flatter distally, allowing to see both laminal parts in the same plane, not undulate; when wet rather flat dorsally-ventrally, not folded along the costa, with the apex hamate, partially incurved towards the stem; 1.9–2.8 × 0.32–0.49 mm, linear-lanceolate to ovate-lanceolate, gradually acuminate to acute at apex, margin entire and plane in all its length; costa blackish brown, ending 3–4 cells below apex, very prominent dorsally, 34.0–36.5 µm wide, strongly keeled proximally, with the lamina at both sides of the costa almost touching each other ventrally; laminal cells in the distal 1/3 of the leaf rounded to oblong or elliptical, 17–19.5 × 9.3–12.5 µm, bulging, thick-walled and collenchymatous, towards the margins becoming short-rectangular, quadrate or oblate, smaller than adjacent interior cells, 5.6–11.0 × 6.0–9.7 µm, less thick-walled and collenchymatous, at mid-leaf morphologically similar to the distal third but smaller, 13.5–17.5 × 6–7.8 µm in the interior of the lamina and smaller towards the margins, 10.4–14.18 × 3.5–6.9 µm, juxtacostal most basal cells distinctly larger than adjacent cells, rectangular, thin-walled, ± hyaline and inflated, similar to ‘cancellina’ in calymperoid mosses, 14.7–17.8 × 6.4–9.7 µm, towards the margins gradually becoming thick-walled and firm, elongated-rectangular, more or less symmetric with straight lumina and walls evenly thickened on both sides, 17–28.5 × 2.5–5 µm, the marginal row consisting of 12–13 thin-walled elongated hyaline cells, 19.5–35.7 × 5.5–10 µm. Perichaetial leaves shorter than the branch leaves, oblong-ovate, 1.27 × 0.27–0.41 mm, apex broadly acuminate, margin entire, apical cells rounded, 9–14.4 × 4.99–7.17 µm; median cells rounded 9.6–12.45 × 7.94–10.95 µm; marginal cells rounded-rectangular, 8–11.28 × 3–5.9 µm; basal cells rectangular-irregularly square, 5–5.9 × 2.66–5.4 µm; all cells clear and smooth. Sporophyte on branch apices; setae 5.3–7 mm long, thick, slightly twisted when dry, reddish brown, smooth, in cross section with 1–2 layers of thick walled epidermal cells, 3–5 × 2.8–5.7 µm, inner cells irregular, 6.3–9.5 × 2.7–5.7 µm; calyptra campanulate, 2.1–2.6 mm long, pleated at base, covering ¾ of the capsule, naked at base and with a few short hairs on the top; capsule globose, completely smooth, non-sulcate, with perfectly circular mouth, brownish when mature, 1.4–1.7 mm long; peristome reduced to a low, papillose membrane, or absent; exothelial cells 26.5–34.5 × 10.4–17.7 µm; spores anisosporous, 41.8–51 µm and 61–72 µm in diameter, densely papillose, globose, young spores green, mature spores brownish to blackish.

Etymology.—The species is named after its type locality, the Nelliampathy hills in the southern Western Ghats.

Distribution and habitat.—The new species is only known from the type collection from an old tree trunk isolated in a grassland at the peak of the Hilltop mount, Nelliampathy hills, Palakkad District, Kerala, India, at an altitude of 1400 m (**Fig. 1**).

Additional specimens studied.—INDIA. Kerala. Palakkad District, Nelliampathy hills, Hilltop, 1400 m, epiphytic, 24 Oct 2023, Sajitha M.S. 195458 (CALI), 195459 (CALI).

Notes.—The new species can be identified by the combination of the following morphological characters: (1) branch leaves strongly curled and flexuous along its costa when dry, unistratose, (2) cells in the distal 1/3 of the leaf bulging, all with smooth walls, neither papillose distally nor tuberculate proximally, (3) a very small area at the juxtacostal extreme base of cells hyaline and larger, similar to the ‘cancellina’ in calymperoid mosses, (4) basal margins with a long, single row of 12–13 elongated, hyaline or pellucid cells, (5) pleated calyptra covering ¾ of the globose capsule, with a few hairs at the beak, (6) peristome teeth reduced, consisting only of a low irregular papillose outgrowth, or absent, and (7) anisospory.

Regarding anisospory, spores were examined from several capsules. In each capsule, two distinct size classes were observed, and no overlap was detected between them. This pattern suggests true anisospory rather than a broad unimodal range of spore sizes.



Figure 3. *Macromitrium nelliampathyanum* Sajitha, Manju & J. Muñoz: **a**, habit in the field; **b–d**, leaves; **e**, perichaetial leaf; **f**, leaf apex; **g**, distal medial cells of leaf; **h**, margin of the leaf at 1/3 from the apex; **i**, margin at mid-leaf; **j**, basal margin of leaf; **k**, Juxtacostal extreme base of cells similar to the 'cancellina'; **l**, marginal row of 10–13 elongated pellucid, linear thin walled cells at basal leaf margins; **m**, **n**, leaves cross sections; **o**, secondary stem cross section [Scale bars: **b–e** = 0.3 mm; **f–j**, **l–n** = 50 µm; **k**, **o** = 100 µm].

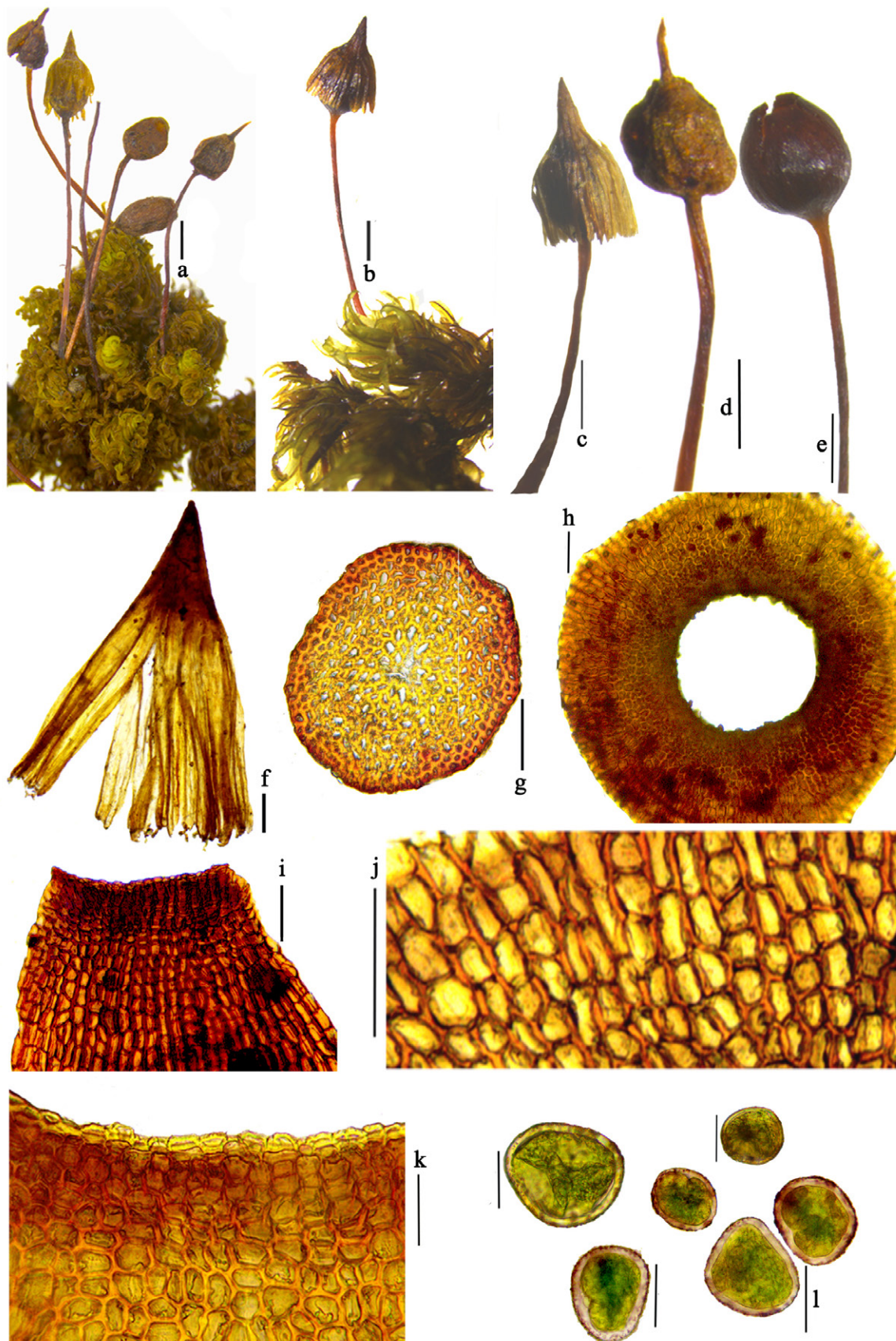


Figure 4. *Macromitrium nelliampathanum* Sajitha, Manju & J. Muñoz: **a**, dry plant with sporophyte; **b**, wet plant with sporophyte; **c**, sporophyte with calyptra; **d**, dry sporophyte with operculum; **e**, globular capsule; **f**, calyptra; **g**, seta cross section; **h**, Capsule mouth from above; **i**, **k**, capsule mouth; **j**, exothecial cells; **l**, anisosporous spores [Scale bars: a–e = 1 mm; f = 0.3 mm; g, k, l = 50 µm; h–j = 100 µm].

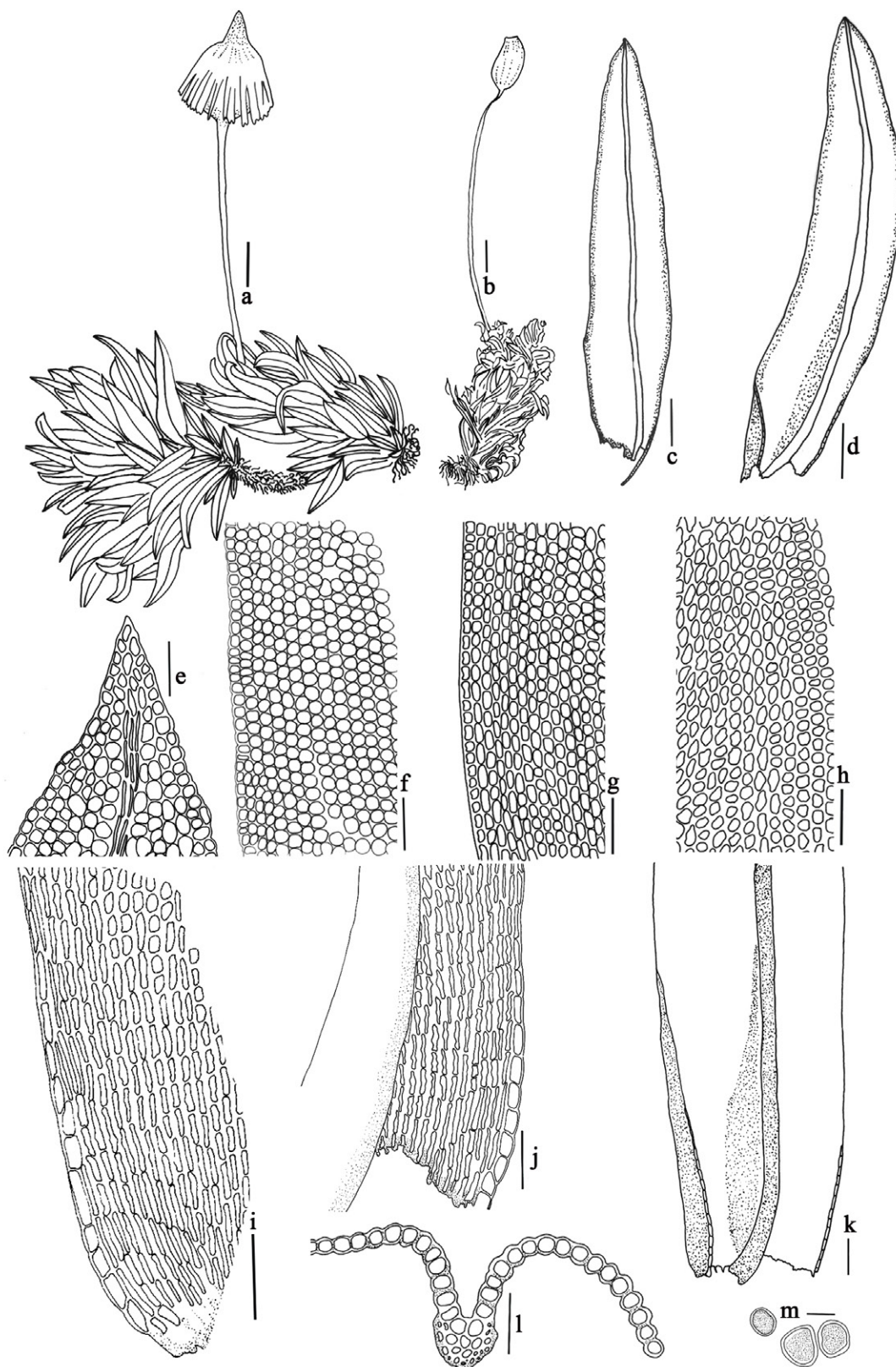


Figure 5. *Macromitrium nelliampathyanum* Sajitha, Manju & J. Muñoz: **a**, wet branches with sporophyte; **b**, dry branches with capsule; **c**, **d**, leaves; **e**, apex of leaf; **f**, distal leaf portion showing marginal and medial laminal cells; **g**, medial portion of leaf showing marginal and medial laminal cells; **h**, basal medial cells of leaf; **i**, **j**, basal marginal leaf cells on either side of leaf; **k**, lower half of the leaf showing the pleat along the costa; **l**, cross section of leaf showing the bulging leaf cells; **m**, anisosporous spores [Scale bars: **a** = 1 mm; **b** = 750 μ m; **c**, **d** = 0,3 mm; **e**–**j**, **l**, **m** = 50 μ m; **k** = 100 μ m] (illustration by Sajitha MS).

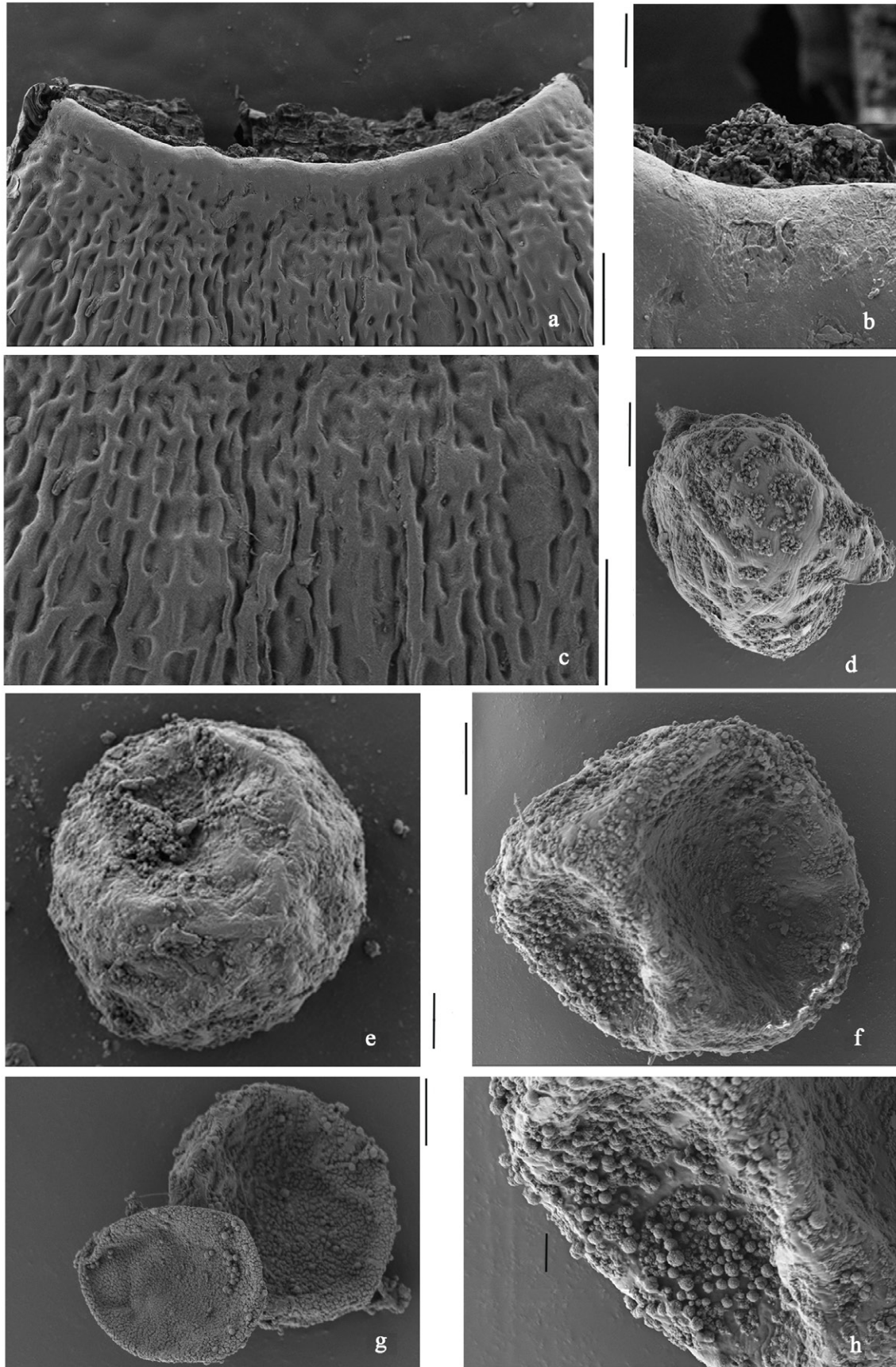


Figure 6. *Macromitrium nelliampathyanum* Sajitha, Manju & J. Muñoz, scanning electron microscope images: **a**, capsule mouth; **b**, exostome; **c**, capsule wall enlarged view; **d–f**, spores; **g**, anisosporous spores; **h**, papillose ornamentation on spore [Scale bars: **a**, **c** = 100 µm; **b**, **d**, **e–g** = 10 µm; **h** = 3 µm].

4. DISCUSSION

The Bayesian analyses show that *Macromitrium nelliampathanum* is related to *Pseudomacromitrium*, a genus close to *Groustiella* (Fig. 2; SF1). However, both molecular and morphological data indicate that *M. nelliampathanum* differs from all other described species in these genera. *Macromitrium blumei* is its closest relative, differing in 5 nucleotide changes in the alignment. Morphologically *M. nelliampathanum* resembles *Groustiella* in having a marginal row of relatively enlarged, elongated, hyaline and thin-walled cells (though these cells are larger in *Groustiella*) and long, narrow, thick-walled cells inside this marginal row (Figs. 3i–k; Fig. 5i). However, the juxtacostal cells at the base are round and thick-walled in *Groustiella*, whereas in *M. nelliampathanum* they are rectangular, thin-walled, ± hyaline and inflated, cancellina-type. Additionally, *Groustiella* species have a calyptra that covers only the upper part of the capsule (Yu & Jia 2023) whereas in the new species the calyptra covers the capsule completely (Figs. 3a; 5a; 6a–c). Our phylogenetic analyses placed *M. nelliampathanum* close to the recently described *Pseudomacromitrium*, as well as to *M. blumei*, an Australasian species with strongly tuberculate proximal cells and a costa excurrent as a stout mucro (Guo *et al.* 2024). The lack of clear phylogenetic separation between *M. nelliampathanum* and *M. blumei* does not preclude the recognition of the new taxon. The morphological evidence, particularly the strongly tuberculate laminal cells and the distinctive mucro of *M. blumei*, provides stable diagnostic characters separating *M. nelliampathanum* from *M. blumei*. On this basis, we consider the new species to be morphologically well circumscribed despite the limited resolution recovered in the molecular analyses. All other species of *Macromitrium* s.l. known from India differ from *M. nelliampathanum* in having papillose distal cells and/or tuberculate proximal cells (Li *et al.* 2020; Guo *et al.* 2024). The morphologically closest species is *M. microstomum* (Hook. & Grev.) Schwägr., widespread in SE Asia and known from Sri Lanka. It has curled leaves that are spirally arranged on the stem when dry, as well as smooth cells throughout. However, it differs in having a well-developed exostome of 16 teeth and a longer seta (15–25 mm), while the new species lacks a peristome (Figs. 4a–b; 6d, h, i).

Macromitrium is a genus that includes more than 300 species distributed throughout the tropical and subtropical regions of the world. Morphologically it is a complex genus, and recent molecular analyses, have led to the segregation of two distinct genera: *Aureomacromitrium* and *Pseudomacromitrium* (Valente *et al.* 2023). The isolation of *M. nelliampathanum* is striking and highlights the need for further combined morphological and molecular studies to understand the diversity of the genus. However, this is beyond the scope of this paper, which focuses on the description of only one, albeit very distinct, new species.

Supplementary information ↑

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Supplementary material

This article includes one supplementary file (SF) available on the journal's website:

SF1: Bayesian majority-rule consensus tree calculated from the results of the analysis of the *trnL-F* data set, including all species of *Groustiella* and *Macromitrium* for which there are sequences available in GenBank, and using *Schlotheimia grevilleana* as outgroup. The Bayesian posterior probabilities are indicated above the branches and maximum likelihood bootstrap values below (without indels = left, regular; with indels coded = right, italic bold). The genera are indicated in the tree as “A” for *Aureomacromitrium*, “G” for *Groustiella*, “M” for *Macromitrium*, and “P” for *Pseudomacromitrium*.

Data availability

List of GenBank accession numbers (*trnL-F*) used for the phylogenetic analysis of *Macromitrium* s.l. Aligned matrices are available <https://doi.org/10.20350/digitalCSIC/17929>.

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Authorship contribution statement

M.S. Sajitha: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Visualization, Writing – original draft, Writing – review & editing.

C. N. Manju: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Dietmar Quandt: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing – review & editing.

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Competing interests

The authors declare that there are no conflicts of interest related to this research.

Statement on the use of Artificial Intelligence

No AI was used in this research.

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APPENDIX

Appendix 1. List of GenBank accession numbers (trnL-F) used for the phylogenetic analysis of *Macromitrium*s.l. Aligned matrices can be downloaded from <https://doi.org/10.20350/digitalCSIC/17929>. Underlined accessions were retained in the core tree shown in Figure 1 and SF1 (supplementary file).

Groutiella chimborazensis: AY636033, MH175888. ***G. mucronifolia***: MN962632, MN962633. ***G. tomentosa***: MH175885, MN962634, MN962635, ON207177. ***G. tumidula***: MH175880. ***Macromitrium angustifolium***: MH730450, MH730451. ***M. argutum***: MN962620, MN962621, MN962622, MN962623, MN962624. ***M. blumei***: MH730452, MK521892. ***M. carionis***: MN245768, MN962600, MN962601, MN962602. ***M. catharinense***: MN962595, MN962596, MN962597, MN962598, MN962599. ***M. cavaleriei***: JX826988, JX826989, JX826992, JX826993, JX826994, JX827000, JX827001, JX827017, JX827019, MH730453, MH730454, PQ201222, PQ201223, PQ201224, PQ201225, PQ201226, PQ201227, PQ201228, PQ201229, PQ201230, PQ201231. ***M. chloromitrium***: ON207179, ON207180, ON207182. ***M. cirrosum***: MN962610, MN962611. ***M. cuspidatum***: MH730455, MH730456. ***M. ferriei***: MH175882. ***M. fimbriatum***: ON207183, ON207185. ***M. fortunatii***: MH730457, MH730458, MH730459, MH730460, MH730461, MH730462, MH730463, MH730464. ***M. guatemalense***: MN245767, MN962618, MN962619. ***M. gymnostomum***: JX826990, JX826991, JX826995, JX826996, JX826999, JX827010, JX827011, JX827012, JX827013, JX827014, JX827015, MH730465, MH730466, MK521894, MK521895, MK521896, MK521897. ***M. incurvifolium***: AF231162. ***M. japonicum***: JX826982, JX826983, JX826984, JX826998, JX827008, JX827009, JX827016, JX827018, MH730467, MH730468, PQ201215, PQ201216, PQ201217, PQ201218, PQ201219, PQ201220, PQ201221. ***M. lanceolatum***: ON207186. ***M. longifolium***: MN962612, MN962613, MN962614, MN962615, MN962616, MN962617. ***M. maolanense***: MK521893. ***M. microstomum***: JX826985, MH730469, MH730470, MN962625, MN962626, MN962627, MN962628, ON207184, ON207190, ON207191. ***M. nanothecium***: ON207181, ON207192. ***M. nelliampathyanum***: This work. ***M. nepalense***: MH730471, MH730472. ***M. ousiense***: JX827007, MH730473. ***M. pallidum***: MN967049, MN967050, MN967051, ON207195, ON207196, ON207197, ON207204. ***M. podocarpus***: MN962608, MN962609. ***M. punctatum***: MN962603, MN962604, MN962605, MN962606, MN962607. ***M. rhacomitrioides***: JX826986, JX826987, JX826997, MH730474, MH730475. ***M. richardii***: MN962629, MN962630, MN962631. ***M. serpens***: ON207198. ***M. soulae***: ON207199. ***M. subtortum***: ON207187, ON207188, ON207189. ***M. sulcatum***: ON207200, ON207201, PQ201212, PQ201213, PQ201214. ***M. taiheizanense***: JX827006. ***M. tosae***: MH730476, MH730477. ***M. turgidum***: MH730478, MH730479. ***M. uraiense***: MH730480, MH730481. ***M. urceolatum***: ON207203. ***Schlotheimia grevilleana***: JX827005.