Bry. Div. Evo. 46 (1): 092–108
https://www.mapress.com/bde
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Article

ISSN 2381-9677 (print edition)
BRYOPHYTE DIVERSITY & EVOLUTION
ISSN 2381-9685 (online edition)

https://doi.org/10.11646/bde.46.1.13

New insights into the genus *Stoneobryum* (Bryophyta: Orthotrichaceae) based on recent collections of the two known species

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Abstract

The morphological traits of the two known species of the genus *Stoneobryum* are reexamined based on newly collected materials. Observations on the Australian species, *S. bunyaense*, are derived from a recent collection made at the type locality, where it has been rediscovered. Those of *S. mirum* are based on recent field collections from numerous locations in eastern South Africa. Comprehensive descriptions of both species and illustrations of their key morphological characters are provided. The new data complement and correct previously available descriptions, especially the original one for the type species of the genus, *S. bunyaense*. *Stoneobryum* arises as a highly differentiated genus, well characterized by sporophytic and gametophytic characters. Its two species are very similar, but nevertheless certainly distinct; an identification key is provided.

Key words: Morphology, mosses, Orthotricheae, Southern Hemisphere, character evolution

Introduction

It is well known that some groups are key for understanding the evolution of certain lineages of organisms (Williams 1966). If the characteristics of one of these groups is poorly understood, this could lead to misinterpreting the evolutionary patterns of the lineage being studied. Such a situation is to be found in *Stoneobryum* Norris & Robinson (1981: 96), one of the 24 genera currently recognised among the Orthotrichaceae (He *et al.* 2022). This family is a diverse and cosmopolitan group of mostly epiphytic mosses, which is still not fully understood from an evolutionary point of view (Draper *et al.* 2022).

Although *Stoneobryum* includes only two species of limited distribution, the nature of its stomata makes it a key genus within Orthotrichoideae (Draper *et al.* 2021; Goffinet *et al.* 2004; Lewinsky-Haapasaari & Hedenäs 1998). This is one of the two major lineages of Orthotrichaceae, characterised by an acrocarpous, rather than cladocarpous, arrangement of perichaetia, and a predominant orthotropic, rather than plagiotropic, growth pattern (Figures 2, 5) (Goffinet & Vitt 1998; La Farge-England 1996). As in *Orthotrichum* Hedwig (1801: 162), and in contrast to the rest of the members of the family, the stomata of *Stoneobryum* are immersed in the capsule exothecium (Figure 3G). Such stomata are termed cryptopore or cryptoporous and, while present in several unrelated lineages of mosses (Frey 2009), they are relatively uncommon (Goffinet *et al.* 2009). However, this is not the only characteristic that makes *Stoneobryum* distinctive.

Stoneobryum is a distinct genus both morphologically (Lewinsky 1993), and phylogenetically (Goffinet *et al.*, 2004; Sawicki *et al.*, 2017; Draper *et al.*, 2021). Morphologically, besides the acrocarpous perichaetial position and cryptoporous stomata, it is characterised by strongly differentiated, sheathing and echlorophyllose perichaetial leaves and small conical calyptra (Lewinsky 1984; Norris & Robinson 1981). The two species of the genus were considered very similar to each other in terms of their vegetative body, differing only by subtle leaf features, but also very different in terms of their sexual characteristics (Norris & Robinson 1981). *Stoneobryum bunyaense* Norris & Robinson (1981: 96) was described as dioicous, with dwarf male gametophytes and bimodal spores, i.e., anisosporous (Lewinsky-

Submitted: 14 Oct. 2023; Accepted by Christine Cargill: 4 Dec. 2023; published: 29 Dec. 2023

Haapasaari & Hedenäs 1998; Norris & Robinson 1981). Conversely, *S. mirum* (Lewinsky 1978: 73) Norris & Robinson (1981: 96) (≡*Orthotrichum mirum* Lewinsky [1978: 73]), is characterised as autoicous and isosporous (Lewinsky 1978; Magill & van Rooy 1998; Norris & Robinson 1981). This is extraordinary, since nanandry is not known from any other representative of Orthotrichoideae, in contrast to it being common among Macromitrioideae, the other subfamily of Orthotrichaceae (Goffinet & Vitt 1998). Furthermore, no other genus within Orthotricheae comprises dioicous and autoicous species (Draper *et al.* 2021, 2022), although this does occur in genera of the other two tribes of the same subfamily (Aguado-Ramsay *et al.* 2022), as well as in genera of Macromitrioideae.

Among the evolutionary characters analysed by Draper *et al.* (2021), there are some other traits that exhibit 'anomalous' behaviors in *Stoneobryum*. As an example, brood bodies are absent, whereas in the other genera with dioicous representatives they are always present. Furthermore, the endostome is reported to lack a connective membrane, which is commonly present in the other members of the subtribe Orthotrichinae.

Stoneobryum was described from plants collected in south-eastern Queensland, eastern Australia (Norris & Robinson 1981). Prior to this study, the type species, *S. bunyaense*, had only been found at one locality in the Bunya Mountains and knowledge of the morphology of the species relies solely on the original collection, which was not particularly rich. By contrast, *S. mirum* is an endemic to eastern South Africa, where it is known from several localities in the KwaZulu-Natal and Eastern Cape provinces. It is particularly common in the Drakensberg Mountains area (Magill & van Rooy 1998; Vanderpoorten & Barker 2004). The descriptions of this South African species have been based on specimens from several populations (Lewinsky 1978; Magill & van Rooy 1998), although it is also not a particularly well-known species due to the scarcity of the collections.

We recently had the opportunity to carry out two collecting campaigns in the territories where the two species of the genus *Stoneobryum* live. We have had success, albeit uneven, in both cases: abundant material of the South African species has been obtained, while the Australian species has been rediscovered, but few specimens have been found. In any case, this has allowed us to obtain material in optimal conditions for a comprehensive assessment of the morphological differentiation of the two species. The aim of the present work is to provide complete and comparable descriptions for both taxa, reassessing their similarities and morphological differences to better understand the evolutionary clues derived from the position of this interesting lineage of orthotrichaceous mosses in the phylogenetic reconstructions.

Material & Methods

The materials studied for this study were collected during 2022 in two collecting campaigns targeting the two areas where the genus *Stoneobryum* is present. In both cases, the selection of localities was biased towards areas that ecologically appeared more favorable for orthotrichaceous mosses, with the location of representatives of *Stoneobryum* being a central objective. Firstly, a bryological expedition was carried out in Eastern South Africa and Lesotho in June and early July. Close to 40 localities were visited, mainly in the Drakensberg escarpment of KwaZulu-Natal Province, the Lesotho highlands, and the Great Escarpment of the Eastern Cape Province. Exploration in Australia focused on the central and southern regions of the easternmost part of the continent, visiting representative localities throughout the territory in several expeditions. In total, over 80 localities were explored. The search for *S. bunyaense* was particularly intensive in the 16 localities studied in the mountains of the subtropical area in northern New South Wales (NSW) and southern Queensland, including three localities in the Bunya Mountains (Figure 1).

The morphological analysis of the samples obtained was carried out in the laboratories of the Autonomous University of Madrid, the University of Valencia, and the National Herbarium of New South Wales. Primarily, light microscopes were used, but in a subsequent phase, scanning electron microscopy (SEM) was employed to confirm details of the ornamentation of the peristomes and spores. For observation with the SEM, completely dried samples were mounted on aluminum studs and then sputter coated with gold/palladium with a thickness of about 200 Å. Micrographs were obtained using a SCIOS 2 FIB-SEM Field Emission SEM at an accelerating voltage of 3.00 kV and a working distance of 7 mm.

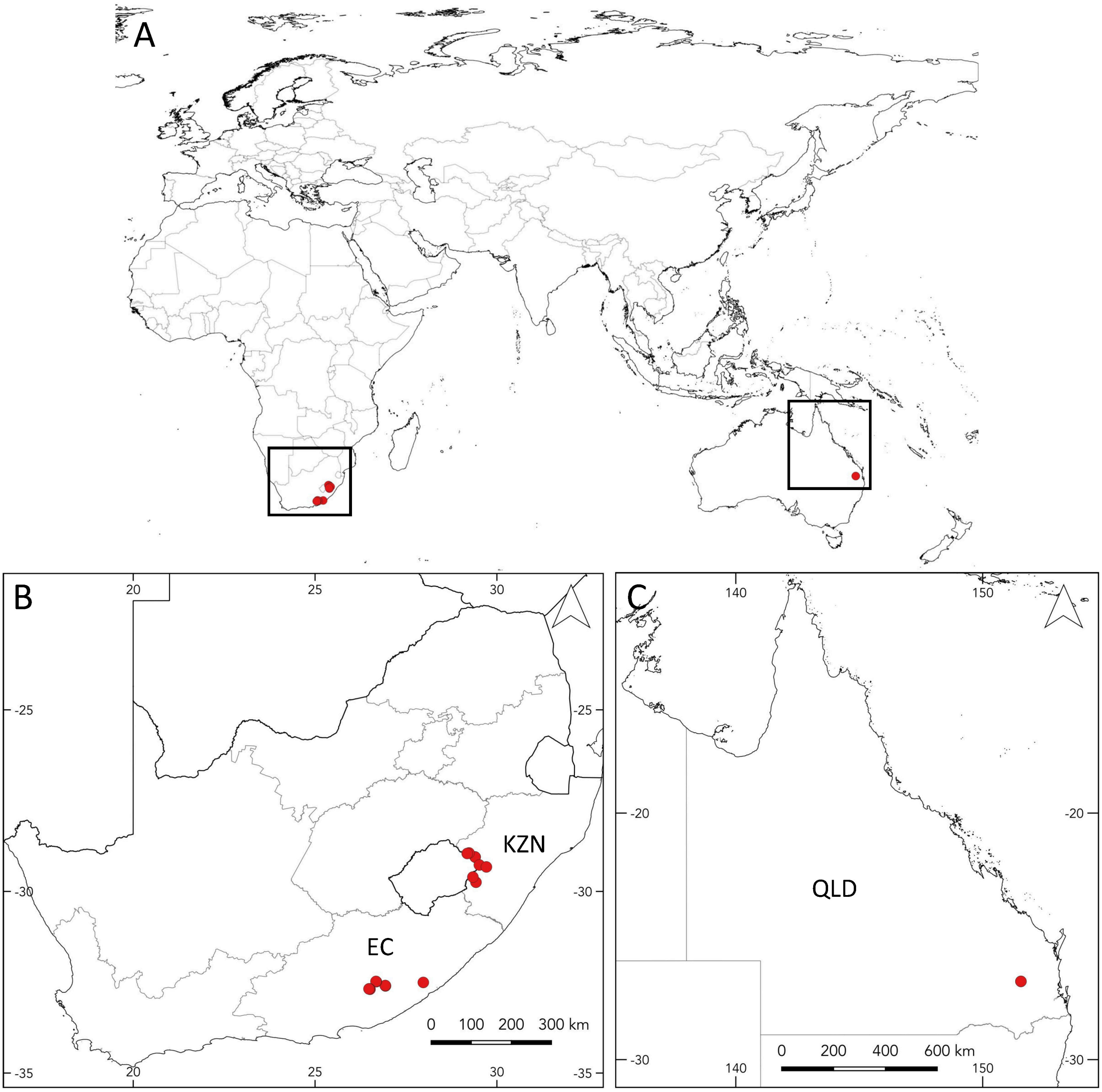

FIGURE 1. Origin of the studied specimens. **A**: General view of the Old World and Australasia, with the studied areas indicated. **B**: Detail of the studied localities of *Stoneobryum mirum*; KZN: KwaZulu-Natal Province, EC: Eastern Cape Province. **C**: Detail of the studied localities of *Stoneobryum bunyaense*; QLD: Queensland.

Selected specimens examined

Stoneobryum bunyaense

AUSTRALIA. **Queensland**: Darling Downs, Bunya Mountains National Park, Burtons Well Walking Track to Mount Kiangarow, 26º49’57”S, 151º32’58”E, 1102 m, on tree twigs in a disturbed and low rainforest, very rich in cryptogamic epiphytes, 08/10/2022, *F. Lara & J. Lara FL2210/16* (MAUAM, BRI); *Ibidem*, 26º49’55”S, 151º32’59”E, alt. 1114 m, on terminal twigs of a fallen branch in a disturbed and low rainforest, very rich in cryptogamic epiphytes, 08/10/2022, *F. Lara & J. Lara FL2210/17* (MAUAM).

Stoneobryum mirum

SOUTH AFRICA. **KwaZulu-Natal**: uThukela Dist., Cathkin Park, uKhahlamba Drakensberg Park, Giants Castle Game Reserve, between Monks Cowl Campsite Park and Nandi’s Falls, 29º03’00”S, 29º24’15”E, 1500 m. On twigs of *Maytenus* sp. 22/05/2022, *R. Garilleti et al. RG2022-09* (MAUAM, PRE); *Ibidem*, 29º03’02”S, 29º24’11”E, 1518 m, on trunk of an isolated small tree, 22/05/2022, *F. Lara et al. FL2205/12* (MAUAM, PRE); Winterton, uKhahlamba Drakensberg Park, Mlambonja valley, ca. Didima Camp Cathedral Peak, 28º56’23”S, 29º14’11”E, 1370 m, on trunk of *Leucosidea sericea* in a scrubland lining the road, 23/05/2022, *R.D. San Román et al. RDSR2205/12* (MAUAM); *Ibidem*, Cathedral Peak area, way to Blue Pools, 28º57’15”S, 29º11’11”E, 1535 m, on the branch of a tree in grassland with scattered trees, 23/05/2022, *R.D. San Román et al. RDSR2205/13* (MAUAM); uMgungundlovu Dist., Highmoor, uKhahlamba Drakensberg Park, Boensmansrivier valley, Giants Castle visitor’s centre surroundings, 29º16’14”S, 29º31’15”E, 1760 m, trunk of a small tree (Araliaceae) in area with ornamental trees and native scrublands, 24/05/2022, *F. Lara et al. FL2205/30* (MAUAM); Mooi River, Glengarry Kamberg, 29º19’28”S, 29º42’49”E, 1570 m, trunk of *Liquidambar styraciflua* in the camping area, 25/05/2022, *F. Lara et al. FL2205/35* (MAUAM); Sisonke Dist., Underberg, Khotso Lodge & Horse Trails, 29º44’46”S, 29º25’38”E, 1535 m, trunk of *Prunus* sp. planted at the campsite, 25/05/2022, *F. Lara et al. FL2205/41* (MAUAM); Mkhomazi Wilderness area, Sani Pass Border Control surroundings, Mkhomazana (Sani) river, 29º36’10”S, 29º20’32”E, 1945 m, *Leucosidea sericea* scrubland on slope next to the stream, on twigs of a vine, 26/05/2022, *N. Matanov et al. NK2205-35a* (Garilleti’s pers. herb.). *Ibidem,* on a dead branch of *Rhus* sp*.,* 26/05/2022, *F. Lara et al. FL2205/46* (MAUAM, PRE). **Eastern Cape**: Amathole Dist., Great Kei Bridge, southern slope near the Kei River, 32º 30’ 19” S 27º 58’ 43” E, alt. 170 m, on twigs of *Acacia karroo* in subtropical thicket (valley bushveld) with *A. karroo*, *Dovyalis rhamnoides* and *Euphorbia tetragona*, 30/05/2022, *R.D. San Román et al. RDSR2205/41* (MAUAM); Amatola escarpment, Hogsback, Swallowtail Caravan and Camping Park, 32º36’04”S 26º56’15”E, 1205 m, on trunk of *Ulmus* sp., 30/05/2022, *F. Lara et al. FL2205/75* (MAUAM, PRE); Hogsback Arboretum, 32º35’23”S 26º56’03”E, 1225 m, trunk of *Liquidambar styraciflua* in a seminatural environment, 31/05/2022, *F. Lara et al. FL2205/81* (MAUAM); Katberg, 32º29’03”S 26º41’13”E, 1030 m, branches of a thorny Celastraceae among planted trees and secondary forest in populated area, 31/05/2022, *F. Lara et al. FL2205/88* (MAUAM, PRE); North of Katberg, 32º28’37”S 26º40’38”E, 1145 m, high branches of *Rhoicissus revoilii* in afromontane lauroid forest dominated by *Podocarpus*, 31/05/2022, *E. San Miguel et al. s.n.* (MAUAM, PRE); Amatola escarpment, Fort Fordyce Nature Reserve, 32º41’31”S 26º30’46”E, 858 m, on branches of small trees in thorny low forest with *Olea europaea* ssp. *africana*, *Rhoicissus revoilii*, *Scutia myrtina* and *Gymnosporia buxifolia*, 01/06/2022, *E. San Miguel et al. s.n.* (MAUAM, PRE); NW of Fort Beaufort, Fort Fordyce Nature Reserve, 32º40’55”S 26º29’28”E, 1140 m, trunk and branches of *Gymnosporia buxifolia* in secundary scrubland in afromontane lauroid forest of *Podocarpus* environment, 01/06/2022, *E. San Miguel et al. s.n.* (MAUAM, PRE); *Ibidem*, 32º40’59”S 26º29’07”E, 1150 m, on trunk of *Kiggelaria africana* in a planted pine copse with scattered native small trees, 01/06/2022, *F. Lara et al. FL2206/08* (MAUAM, PRE).

Results

The discovery of populations and acquisition of *Stoneobryum* samples has been highly unequal in the two studied territories. The Australian species, *S. bunyaense*, was found in only one locality, the *locus classicus* at Bunya Mountains, from where it was described over 40 years ago (Norris & Robinson 1981). No subsequent reports of new collections from this or other locations are known, except for the present study. In our field campaign, only a few specimens were found on two unidentified trees, both in a disturbed rainforest very rich in cryptogamic epiphytes, at similar elevations (1102 and 1114 m). The two samples, although scarce, comprised several colonies with fully developed plants, including mature sporophytes. No further specimens were found in other localities within the same mountains or in similar environments in the northern NSW ranges.

In the case of *Stoneobryum mirum*, more than 30 samples were obtained from 16 sites, all of them within South Africa. These locations span a wide elevational range: (170–)850–1760(–1945) m, although more than half were situated between 1100 and 1600 m. They represent diverse habitats, primarily ranging from humid Afromontane forests to dry succulent and spiny thickets found in river valleys of the Eastern Cape (valley bushveld). The host trees and shrubs were highly varied. The identified native species include *Acacia karroo* Hayne (1827: 33), *Buddleja* sp., *Gymnosporia buxifolia* (Linnaeus 1753: 197) Szyszyłowicz (1888: 34), *Halleria lucida* Linnaeus (1753: 625), *Kiggelaria africana* Linnaeus (1753: 1037)*, Leucosidea sericea* Ecklon & Zeyher (1836: 265), *Maytenus* sp., *Rhoicissus* *revoilii* Planchon in Candolle & Candolle (1887: 469), *Schotia* sp., and *Searsia chirindensis* (Baker f. in Rendle *et al.* 1911: 49) Moffett (2007: 167). Several samples were found on various non-native trees such as *Acer* sp., *Liquidambar styraciflua* Linnaeus (1753: 999), *Prunus* sp., *Quercus robur* Linnaeus (1753: 996), and *Ulmus* sp. Populations of *S. mirum* varied in density, from abundant to scant, with no clear correlation between abundance and altitude, forest type, or predominant host tree species. Overall, the collected material is abundant, showcasing various developmental stages of the mosses, always with individuals containing mature or nearly mature sporophytes.

Species descriptions

Stoneobryum bunyaense D.H.Norris & H.Rob., The Bryologist 84: 96. 1981. (Figures 2–4)

Type: AUSTRALIA, Queensland, Bunya Mtns. Natl. Pk., on branches high in tree in open *Eucalyptus* forest along trail from Burtons Well to Mt. Kiangarow, elev. 1000–1200 m, *D. Norris 35310* (Holotype: BRI; isotypes: HSC, US 70599 images seen!).

Plants 0.2–0.6(–0.7) cm tall, in tufts or small cushions up to 1 cm in diameter, bright olive green above, dark green to brownish below. **Stems** pentagonal in section, with 2(–3) outer layers of smaller cells with light orange slightly thickened walls and narrow lumina; **axillary hairs** with 1–2 short colored basal cells and 1–3 oblong hyaline distal cells. **Rhizoids** in basal parts of stems, brownish to reddish-brown, thick-walled, smooth, frequently with bulbous ends. **Leaves** (1.3–)1.6–2.6(–2.9) × (0.2–)0.4–0.5(–0.6) mm, irregularly and openly contorted when dry, patent to spreading, somewhat flexuous when moist, very variable in shape, ovate-oblong to lingulate or spathulate, often slightly constricted below middle (pandurate), at base frequently concave in juxta-costal region, plane to slightly carinate but always with prominent costa dorsally when dry; **leaf apex** acute to obtuse, frequently mucronulate, rarely shortly acuminate or rounded; **costa** single, ending below apex to percurrent, 55–70 µm wide at base, 45–55 µm wide at mid-leaf; **leaf margins** entire, in young leaves slightly crenulate, plane or narrowly recurved in lower 2/3 of leaf, frequently on one side only; **lamina** unistratose throughout; **upper and median leaf cells** almost isodiametric to somewhat elongate, (8–)11–14(–15) × (8–)9–11(–12) µm, with moderately thickened walls, smooth or minutely unipapillose, papillae very low and simple, best seen at leaf margins; **basal cells** short to long rectangular, in mature leaves differentiated in three bands, a usually broad central band of firm, brownish cells, with walls moderately thickened, slightly sinuous to nodulose, (15–)23–50(–60) × (9–)12–15(–16) µm, a narrow to broad paracostal region, of lax, hyaline cells with walls thin and straight, (18–)30–60(–89) × (8–)12–18(–22) µm, and a narrow marginal band, 1–3 rows wide, of firm, hyaline cells with walls thin and straight, (12–)14–33(–42) × (10–)12–15(–18) µm. Brood bodies lacking.

Cladautoicous. **Perigonia** bud-shaped, with few antheridia, terminal (pseudolateral) on branches and main axes; **perigonial leaves** light brown, ovate-triangular, 0.4–0.6 mm long, with acute apex and weak or no nerve. **Perichaetia** terminal, with few archegonia. **Perichaetial leaves** strongly differentiated, lingulate to oval-lingulate, plane to slightly concave or carinate, hyaline, with more or less weak, green to brown nerve, ending below apex to percurrent, margin plane, apex rounded, 1.3–1.6 × 0.4–0.6 mm, the inner perichaetial leaves tightly adpressed to the capsule and sometimes completely hyaline, more or less frayed at apex, the external ones with a distal part chlorophyllose, similar in areolation to that of vegetative leaves; hyaline perichaetial leaf cells elongated trapezoid to long rhomboidal, 39–127 × 9–18 µm, near base frequently long rectangular, 39–113 × 10–20 µm, all cells firm, with walls thin and straight; cells at proximal extreme with walls moderately thickened, colored, sometimes sinuose. **Vaginula** cylindric, 300–350 µm long, naked. **Calyptra** conic, covering distal 1/3 of capsule, 0.6–0.8 mm long, orange-brown, hyaline below, easily disintegrated before falling off, not plicate, evenly hairy, with hyaline to yellowish, long, uniseriate, sparsely papillose hairs, overpassing the beak up to 0.3 mm. **Seta** very short, protruding 50–100 µm out of vaginula. **Capsule** dark brown, emergent from perichaetial leaves when dry, overpassed by vegetative leaves when wet, ovoid when moist, when dry ovoid-urceolate, contracted towards mouth, but not or slightly constricted below it, strongly 8-ribbed in the upper half, (1.1–)1.2–1.4 mm long, including a 0.4 mm neck, abruptly contracted to seta; **exothecial cells** rectangular, with yellowish, slightly thickened walls; **exothecial bands** well differentiated in the distal 1/3 of urn, of (3–)4 rows of darker cells with more thickened walls, subtly differentiated down to the base of the urn; **suboral ring** differentiated, of (3–)5 rows of obscure, small, rounded to oblate cells**;** **stomata** immersed, barely to half covered by slightly differentiated exothecial cells, located in the neck. **Operculum** 0.4–0.5 mm in diameter, convex, almost rounded to mamillate, cream colored with a narrow orange basal rim of 1 row of cells. **Peristome** double; **prostome** not seen; **exostome** of 8 pairs of teeth, firmly united, not splitting with age, reflexed and attached to the exothecium when dry, light cream, contrasting

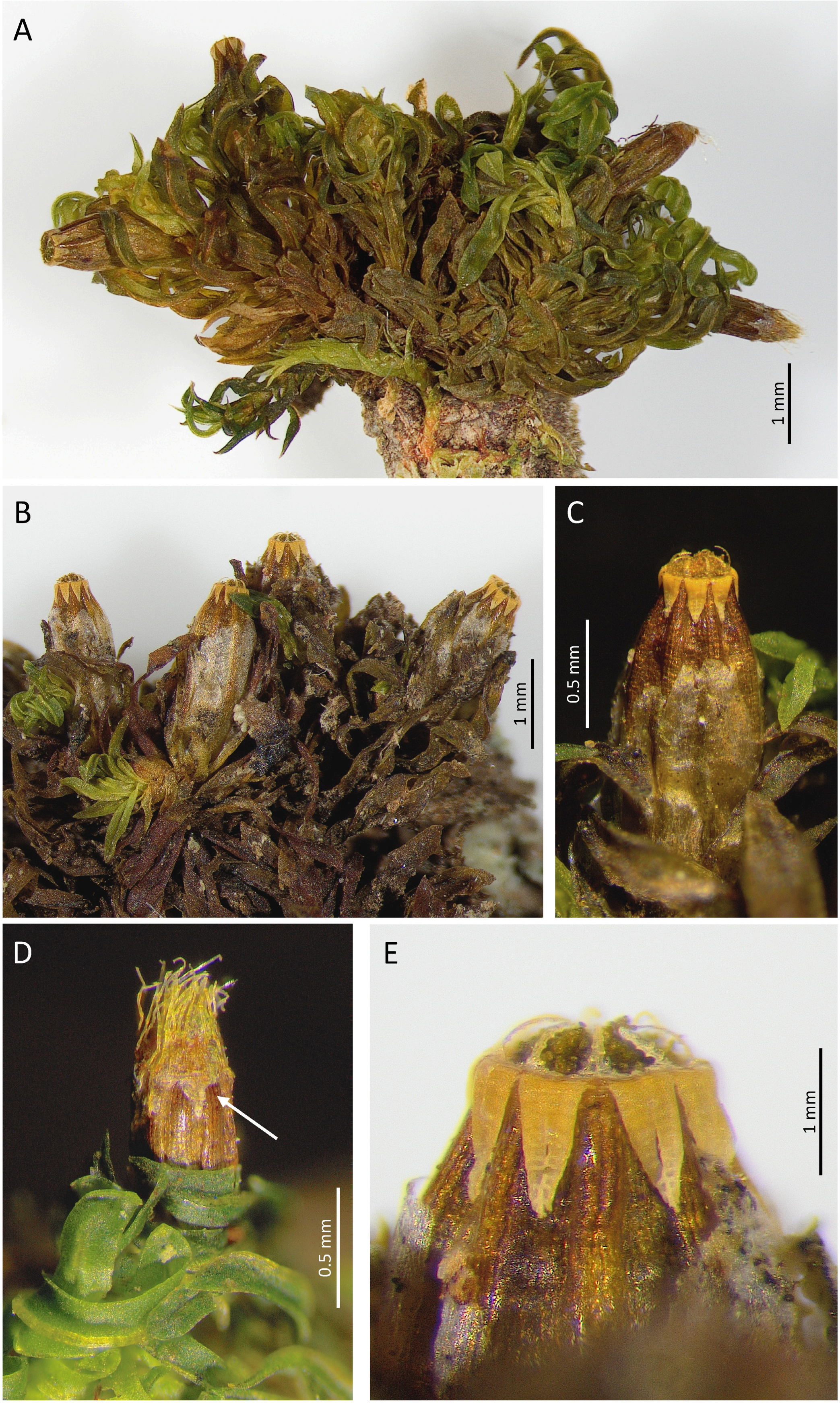

FIGURE 2. *Stoneobryum bunyaense*. **A**: Habit of a cushion growing on a twig. **B**: Detail of the habit. **C**: Mature capsules releasing spores; note the completely hyaline perichaetial leaves enclosing the capsule. **D**: Capsule with calyptra; note the base of the calyptra in the process of disintegrating (arrow). **E**: Detail of the peristome with the endostomial connective membrane protruding from the mouth. A, D: *F. Lara 2210-16* (MAUAM); B, C, E: *F. Lara 2210*-17 (MAUAM). Photographs by R. Garilleti.

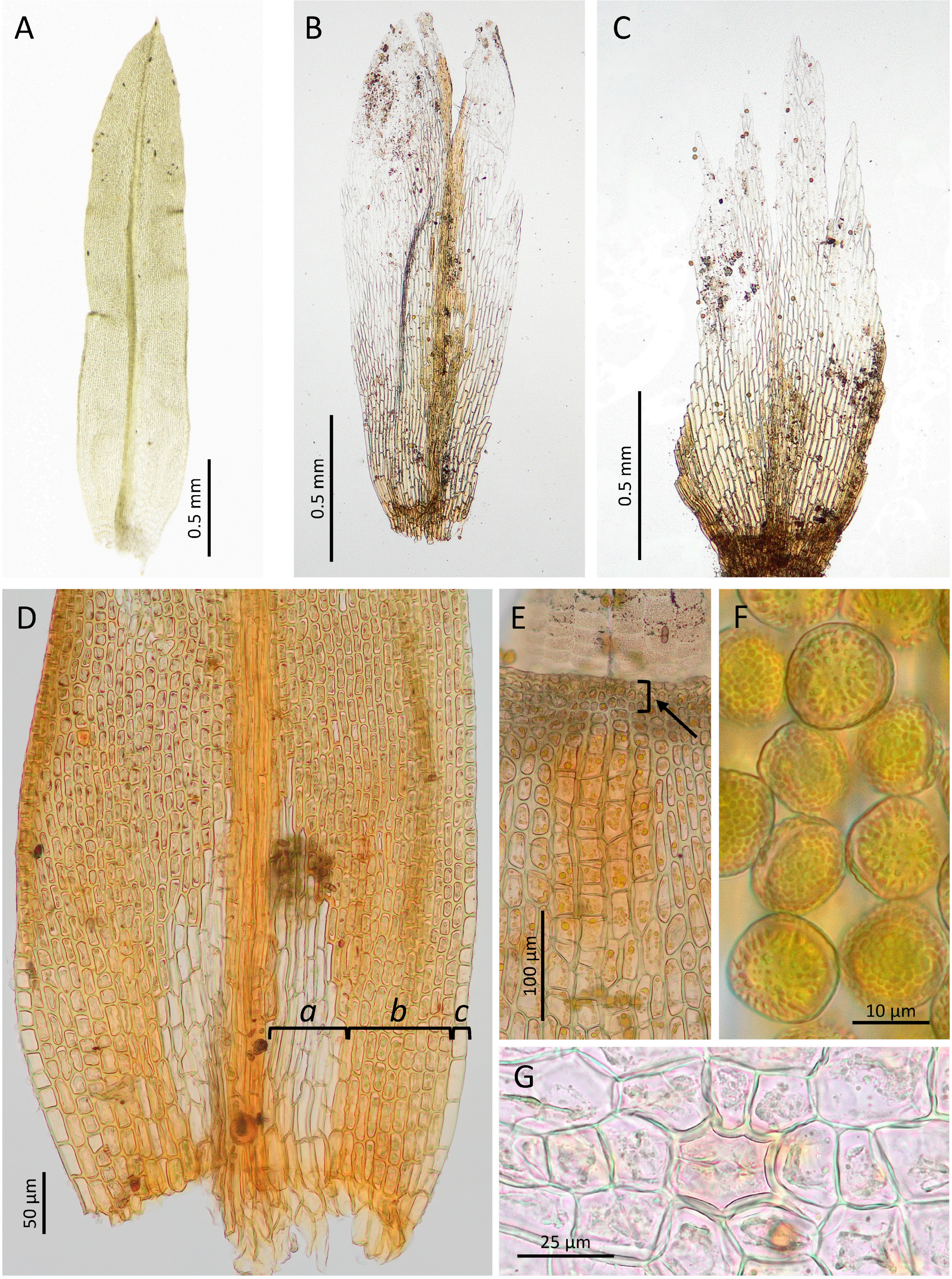

FIGURE 3. *Stoneobryum bunyaense*. **A**: Vegetative leaf. **B–C**: Perichaetial leaves naturally damaged, with different costa development. **D**: Base of a vegetative leaf showing the three bands of differentiated cells, with hyaline cells in the juxta-costal area (***a***) and at margin (***c***), and a central band of firm chlorophyllose cells (***b***). **E**: Upper part of the exothecium, with exothecial band and visible suboral ring (arrow and bracket). **F**: Spores in different positions, the one in the basal left corner is in proximal view, the one just to its right is in distal view, and the one above the former clearly shows the equatorial ridge. **G**: Stoma and surrounding exothecial cells. All from *F. Lara 2210-17* (MAUAM). Photographs by R. Garilleti.

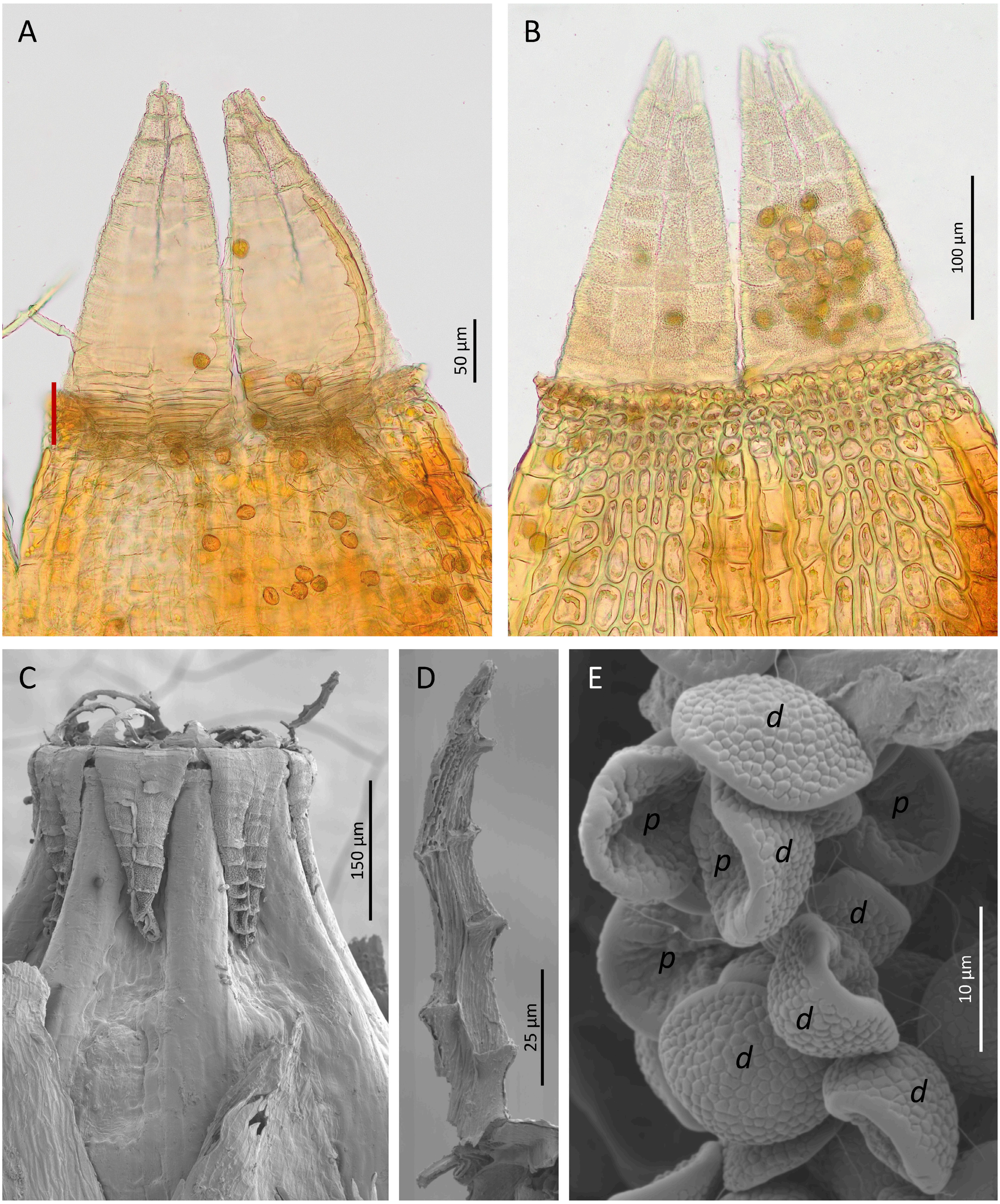

FIGURE 4. *Stoneobryum bunyaense*. **A**: Inner view of peristome, showing endostome segments and endostomial connective membrane; red bar indicates the width of the connective membrane. **B**: External view of exostome. **C**: Upper part of a mature capsule. **D**: Ornamentation of the inner side of an endostomial segment. **E**: Spores with proximal (***p***) and distal (***d***) faces indicated. All from *F. Lara 2210-17* (MAUAM). Photographs by R. Garilleti.

with the color of the urn, 190–250 µm long; **outer peristomial layer** (OPL) densely and finely papillose throughout, in distal half with some vertical lines interspersed with papillae; **exostome primary peristomial layer** (PPL) finely ornamented, with longitudinal and transverse lines and some intercalate papillae below, papillose with occasional longitudinal lines towards apex, distal trabeculae tall and thickened; **endostome** of 8 segments, hyaline, linear, shorter than teeth, 100–140 µm long, united by a connecting membrane of 4–5(6) rows of long rectangular, totally smooth cells; PPL of segments faintly carinate, almost smooth, with scattered thickenings; inner peristomial layer (IPL) of segments symmetrically biseriate, neatly striolate by longitudinal lines and with papillae near tip. **Spores** unimodal in size, (10–)13–15(–16) µm, light brown, more or less spherical, with low and uneven ornamentation on both halves, distal half with dense blunt papillae, proximal half less dense, with anastomosed and radially aligned papillae forming a continuous ridge towards the equatorial zone.

Stoneobryum mirum (Lewinsky) D.H.Norris & H.Rob., The Bryologist 84: 98. 1981. (Figures 5–7)

≡ *Orthotrichum mirum* Lewinsky, Botanisk Tidsskrift 72: 73. 1978. Type: SOUTH AFRICA, Natal, Scheeper's Neek, Arcadia. On trees, *T.R. Sim 10.104* (Holotype: PRE).

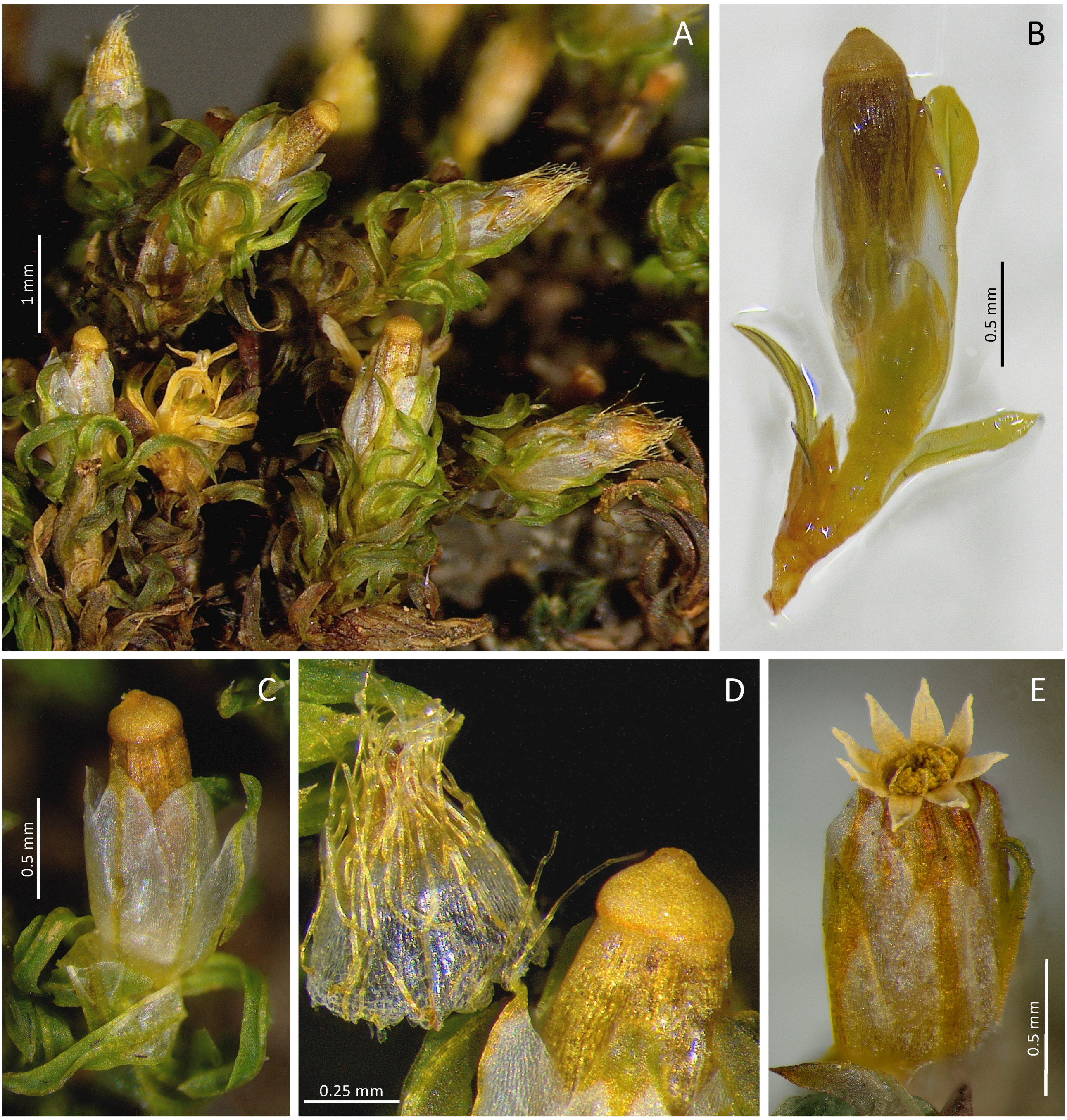

FIGURE 5. *Stoneobryum mirum*. **A**: Habit. **B**: Terminal branch showing a sporophyte and a perigonium, both in terminal (pseudolateral) positions. **C**: A mature capsule surrounded by strongly differentiated perichaetial leaves. **D**: Calyptra and close-up of the operculum. **E**: Capsule immersed in the perichaetium, just after the operculum detachment, with spreading exostome. All from *N. Matanov 2022-35a* (Herb. Garilleti). Photographs by R. Garilleti.

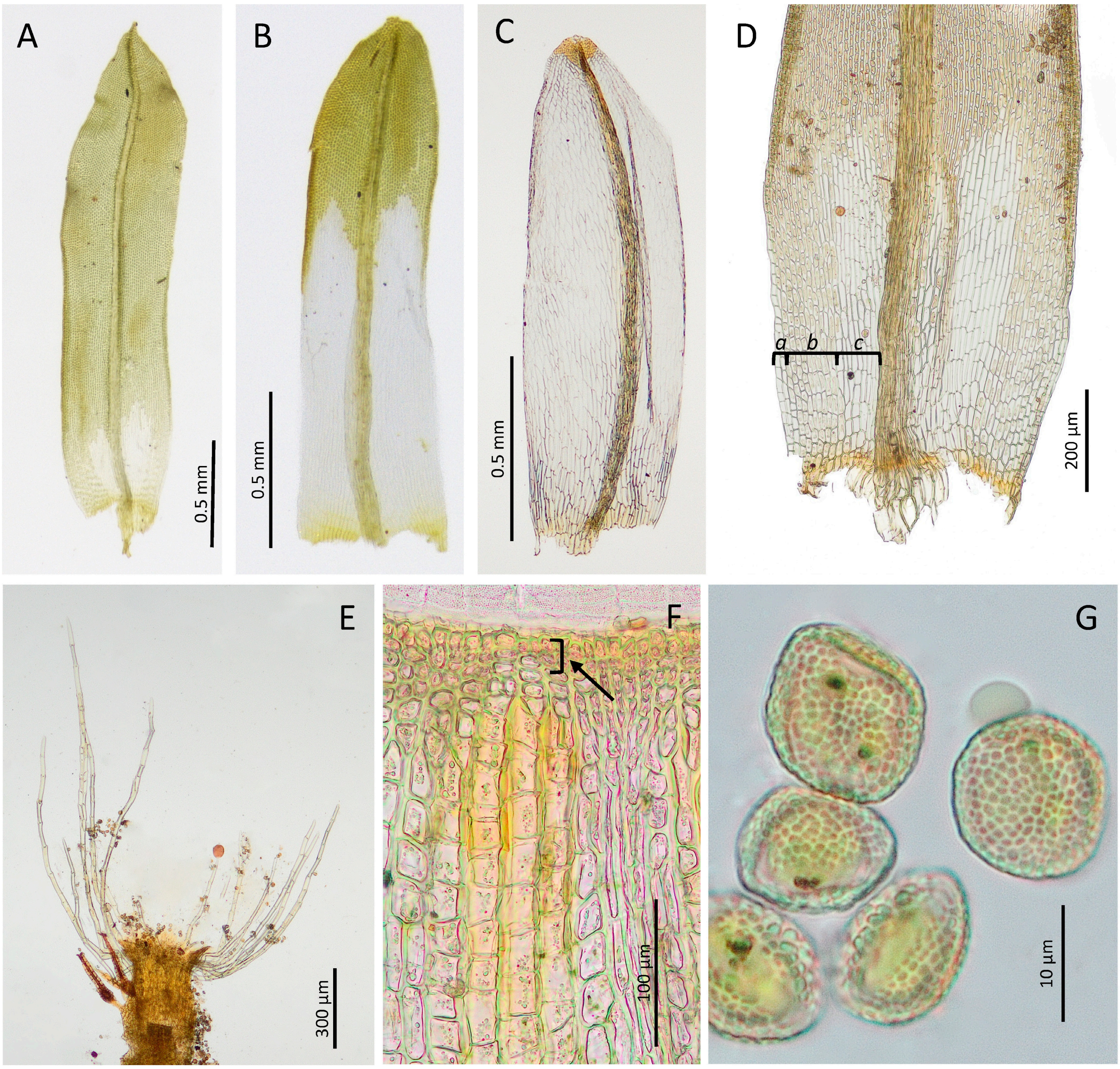

FIGURE 6. *Stoneobryum mirum*. **A**: Vegetative leaf. **B**: Outer perichaetial leaf. **C**: Inner perichaetial leaf; note the well-developed costa and the orange colored apex. **D**: Base of a vegetative leaf showing the differentiated cell bands, with one to several rows of hyaline marginal cells (***a***), a central band of firm chlorophyllose cells (***b***), and hyaline paracostal cells forming a broad and clearly visible area (***c***). **E**: Vaginula with the characteristic crown of curved hairs. **F**: Upper part of the exothecium, with exothecial band and suboral zone (arrow and bracket). **G**: Spores. A, B, C, F: *N. Matanov 2022-35a* (Herb. Garilleti); D, E: *F. Lara* 2205-75 (MAUAM); G: F. Lara 2205-46 (MAUAM). Photographs by R. Garilleti.

Plants 0.5–1.1(–1.2) cm tall, in tufts or cushions up to 2 cm in diameter, pale to dark olive green above, brownish below. **Stems** pentagonal in section, with 2(–3) outer layers of smaller cells with light orange slightly thickened walls and narrow lumina; **axillary hairs** with 1–2 short colored basal cells and 1–3 oblong hyaline distal cells. **Rhizoids** in basal parts of stems, brownish to reddish-brown, thick-walled, smooth, not swollen at ends. **Leaves** (1.3–)1.8–2.6(–2.9) × (0.2–)0.4–0.6 mm, irregularly and openly contorted when dry, patent to spreading, somewhat flexuous when moist, variable in shape, mostly lanceolate-spathulate or oblong-lanceolate, frequently somewhat constricted below middle becoming lanceolate-panduriform, at base more or less concave especially in juxta-costal region, lamina more or less carinate with dorsally prominent costa when dry; **leaf apex** acute to shortly acuminate, less frequently obtuse and mucronulate, rarely rounded; **costa** single, ending below apex to percurrent, 50–65 µm wide at base, 40–56 µm wide at mid-leaf; **leaf margins** entire, plane or variably recurved in lower 2/3 of leaf, frequently on one side only; **lamina**

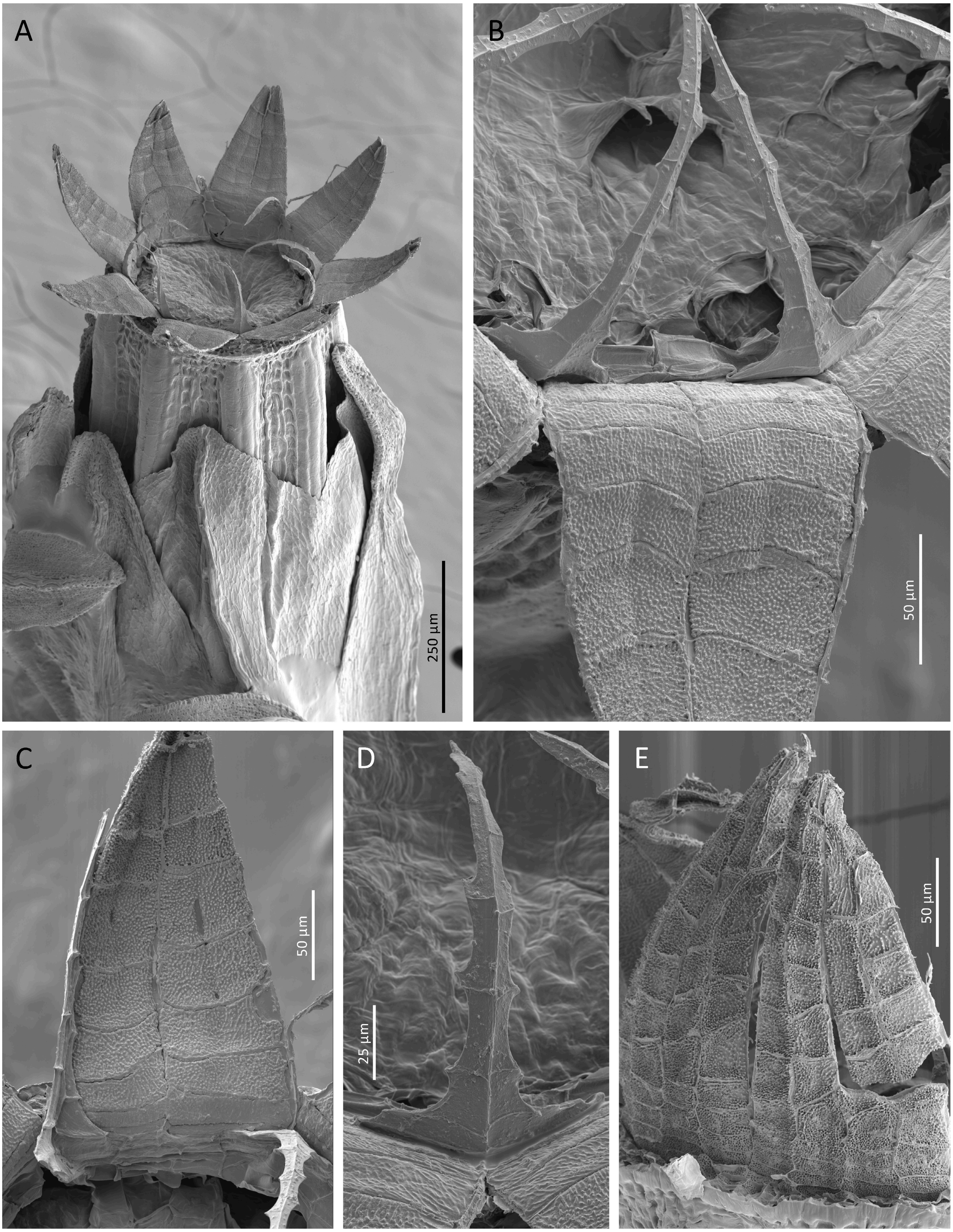

FIGURE 7. *Stoneobryum mirum*. **A**: SEM view of the upper part of a mature individual, with a capsule partially surrounded by the perichaetial leaves, showing the peristome at an intermediate opening; note that the spore sac is intact closing the mouth. **B**: Detail of the previous peristome, showing the base of the exostomial teeth and the endostome connective membrane joining the segments. **C**: Partial view of the peristome from inside, showing an endostome segment attached to the teeth and a second in its typical incurved position. **D**: External side of a segment. **E**: Partial view of the outer side of the exostome. All from *N. Matanov 2022-35a* (Herb. Garilleti). Photographs by R. Garilleti.

unistratose throughout; **upper and median leaf cells** almost isodiametric to somewhat elongate, (8–)10–17(–22) × (8–)10–15(–19) µm, with moderately thickened walls, smooth or minutely unipapillose, papillae very low and simple, best seen at leaf margins; **basal cells** short to long rectangular, in mature leaves differentiated in three bands, a usually broad central band of firm, lightly brown or green cells, with walls moderately thickened, straight to sinuose, rarely nodulose, (14–)22–48(–63) × (10–)11–15(–17) µm, a narrow to broad paracostal region, of lax, hyaline cells with walls thin and straight, (19–)31–54(–73) × (7–)12–17(–22) µm, and a narrow marginal band, 1–4(–6) rows wide, of firm, hyaline cells with walls slightly thickened and straight, 18–36(–50) × (7–)9–15(–18) µm. Brood bodies lacking.

Cladautoicous. **Perigonia** bud-shaped, with few antheridia, terminal (pseudolateral) on branches and main axes; **perigonial leaves** greenish to brown, ovate-triangular, 0.4–0.6 mm long, with acute apex and well-developed nerve. **Perichaetia** terminal, with few archegonia. **Perichaetial leaves** strongly differentiated, forming a showy, cup-shaped to campanulate, whitish structure surrounding the sporophyte, lingulate to oval-lingulate, concave, mostly hyaline, green at distal part, with weak to well-developed green nerve, with margin mostly plane narrowly recurved in green distal parts, apex rounded, sometimes irregularly toothed, costa ending below apex to percurrent, (1.2–)1.6–2.1 × 0.4–0.6(–0.7) mm, the inner perichaetial leaves not attached nor touching capsule, hyaline with a weak green nerve and chlorophyllose tip, rarely completely hyaline, the external ones with strong green nerve, at distal 1/3–1/5 chlorophyllose areolation similar to that of vegetative leaves; hyaline perichaetial leaf cells elongated rectangular to trapezoid, more rarely rhomboidal, (17–)22–95(–124) × (7–)10–17(–19) µm, firm, with straight walls, near base frequently long rectangular, (34–)43–104(–127) × (8–)13–17(–22) µm, somewhat lax, with walls slightly thickened and straight; cells at proximal extreme somewhat differentiated with walls slightly thicker, yellowish. **Vaginula** cylindric, 250–350 µm long, with several to many long, uniseriate, slightly papillose, hyaline hairs characteristically curved and located in upper part of vaginula embracing ochrea and basal part of capsule. **Calyptra** conic, covering distal 1/3 of capsule, 0.7–1.0 mm long, hyaline below, orange-brown to the top, with dark tip, remaining intact until falling off, not plicate, evenly hairy, with yellow to orangish or hyaline, long, uniseriate, sparsely papillose hairs, overpassing the beak up to 0.3 mm. **Seta** very short, protruding 20–60 µm out of vaginula. **Capsule** brown, shortly emergent from perichaetial leaves when dry, overpassed by vegetative leaves when wet, ovoid when moist, when dry cylindric to ovoid, not contracted towards mouth, not or slightly constricted below it, strongly 8-ribbed throughout, (1.4–)1.6–1.8 mm long, including a 0.4–0.5 mm neck, abruptly contracted to seta of which the apical part is hidden in a hollow; **exothecial cells** quadrate to rectangular, with hyaline, thin to slightly thickened walls; **exothecial bands** differentiated in the distal 1/3–2/3 of urn, of 3–4 rows of brownish cells with somewhat thickened walls, near mouth with darker and thicker walls; **suboral ring** slightly differentiated, of 2–3 rows of concolorous, small, rounded to oblate cells**; stomata** immersed, barely covered by slightly differentiated exothecial cells, located in the neck. **Operculum** 0.4–0.5 mm in diameter, convex, rounded to mamillate, cream to brownish with no colored basal rim or with a very narrow light orange border. **Peristome** double; **prostome** not seen; **exostome** of 8 pairs of teeth, partially splitting with age, reflexed and attached to the exothecium when dry but frequently held erect and closing the mouth in old capsules, light cream, contrasting the color of the urn, 210–280 µm long; **outer peristomial layer** (OPL) densely and finely papillose throughout, in distal half with some vertical lines scattered among papillae; **exostome primary peristomial layer** (PPL) finely ornamented with longitudinal and transverse lines below, towards apex distinctly papillose, distal trabeculae somewhat thickened; **endostome** of 8 segments, hyaline, linear, shorter than teeth, 125–200 µm long, united by a connecting membrane of 3–4 rows of rectangular, totally smooth cells; PPL of segments faintly carinate, almost smooth or with scattered verrucae; inner peristomial layer (IPL) of segments symmetrically biseriate, rugose to minutely striolate-papillose. **Spores** unimodal in size, (9–)12–15(–18) µm, light brown, more or less spherical, ornamented with low and blunt papillae, less densely arranged in proximal half and anastomosing in a continuous equatorial ridge.

Discussion

The comprehensive morphological analysis of recently collected *Stoneobryum* material has yielded critical data that complement or even rectify previous observations regarding the two recognized species within the genus. These new findings carry significant implications, particularly concerning the Australian species, *S. bunyaense*. Some discrepancies from the original description of this species (Norris & Robinson 1981) could be ascribed to morphological variability, such as differences in plant size. However, several of our observations challenge qualitative characteristics previously considered distinctive features of *S. bunyaense*, which is relevant since this was established as the type species of the genus (Norris & Robinson 1981).

The most significant revision regarding the characteristics of *Stoneobryum bunyaense* concern the sexuality of the plants. Norris & Robinson (1981) described the species as dioicous, showing male plants with terminal perigonia that were unbranched and smaller than the female plants. The male plants would appear scattered among the female plants or even developing in their leaf axils as dwarf males. The supposed dioicous condition was reinforced by the interpretation that spores exhibited bimodal size distribution (anisospory), a pattern found in various genera of Orthotrichaceae (Vitt 1968). This has been consistently maintained in subsequent treatments (Ramsay *et al.* 2006), shaping the analysis and interpretation of certain evolutionary patterns (Draper *et al.* 2021; Lewinsky-Haapasaari & Hedenäs 1998). However, the newly examined specimens of *S. bunyaense* are conclusively autoicous. The plants are always hermaphroditic, with main stem ceasing growth after the formation of a terminal perigonium or a perichaetium; growth then continues with the formation of successive and relatively short lateral branches, which also cease their growth after the formation of terminal perichaetia or perigonia—a sympodial chain of connected modules as described by La Farge-England (1996). This represents a cladautoicous arrangement of gametangia, akin to what occurs in *Orthotrichum* s. str. (Lara *et al.* 2016). As in *Orthotrichum*, the perigonia frequently remain arranged in a pseudo-lateral position following the development of axes that function as false monopodia. Additionally, the examined capsules in the new collections of *S. bunyaense* contained only unimodal spores (Figure 3F), almost all of them measuring 13–15 µm in diameter, in no instance well exceeding 20 µm in size, as was previously described for the large spores in the presumed bimodal distribution (Norris & Robinson 1981). The autoicous condition and the development of a single spore type in *S. bunyaense* are consistent with what has been previously reported (Lewinsky 1978; Magill & van Rooy 1998) and is now confirmed for *S. mirum*. According to this result, the genus *Stoneobryum* could be defined as autoicous and isosporous.

The study of the new specimens has revealed additional features common to the two species of *Stoneobryum*, all of which would thus characterize the genus. With regards to the gametophyte, these features are associated with both vegetative and perichaetial leaves, as well as calyptras. The vegetative leaves are distinctive for being contorted when dry (Draper *et al.* 2021; Norris & Robinson 1981). Notably, the leaf lamina cells are smooth to scarcely papillose, while the basal cells are differentiated into three more or less evident bands. Norris & Robinson (1981) accurately described the median and upper cells of the leaf as 'smooth to slightly mamillate', although various authors have subsequently considered them to be entirely smooth (Frey & Stech 2009; Lewinsky-Haapasaari & Hedenäs 1998; Magill & van Rooy 1998). While it is true that the appearance of these leaf cells is essentially smooth, from an evolutionary perspective it is important to note that these cells can exhibit low papillae. In the closely related and diverse genus *Orthotrichum*, some species also exhibit slight or absent leaf cell papillosity (Lewinsky 1993). However, within Orthotrichaceae, only two genera are comprised of only species with completely smooth leaf cells, and both are phylogenetically distant from *Stoneobryum*: *Codonoblepharon* Schwägrichen (1824: 142), within Orthotrichoideae, and *Schlotheimia* Bridel (1812: 16), within Macromitrioideae, each segregated into an independent tribe within their respective families (Aguado-Ramsay *et al.* 2022).

Even more intriguing is the nature of the leaf basal cells in *Stoneobryum* (Figures 3D, 6D). Each half of the leaf base reveals three distinctive longitudinal bands, exhibiting distinct areolation in terms of color, size, cell walls, and firmness—an aspect that has been overlooked until now (Frey & Stech 2009; Norris & Robinson 1981). The marginal basal cells are hyaline and firm, forming a thin but clearly visible outer band, often consisting of a single row of cells. These cells are well differentiated, relatively short, with thin walls, and entirely hyaline, i.e., resembling those of *Ulota* Mohr (1806: 540) and related genera (Draper *et al.* 2021)—however, they lack the characteristic thickened transverse walls seen in many species of these groups. Towards the center, a primary band develops, usually spanning most of the width of the base, composed of firm chlorophyllose cells. These cells have relatively thick walls that are variably sinuose or nodulose. Finally, a paracostal band of prosenchymatose cells of variable width is differentiated, made up of slightly longer and hyaline cells, with no sinuose thin walls. The particular constitution of this paracostal band often results in a concave and triangular juxta-costal basal region—very similar to what is characteristic in species of *Macrocoma* (Hornsch ex Müller 1845: 522) Grout (1944: 4), a genus in Macromitrioideae (Fife 2017; Vitt 1973). While the differentiation into three distinct basal cell bands is easily discernible in many *S. bunyaense* leaves, it is well visible only in some adult leaves in *S. mirum*. Notably, the absence of cell differentiation throughout the basal area is common in young leaves. In any case, the differentiation into three types of bands of the basal cells of mature leaves is a unique characteristic of *Stoneobryum*, unparalleled among Orthotrichaceae.

The strong differentiation of perichaetial leaves in *Stoneobryum* has consistently been emphasized as a fundamental characteristic of the genus (Frey & Stech 2009; Lewinsky-Haapasaari & Hedenäs 1998; Magill & van Rooy 1998; Norris & Robinson 1981; Ramsay *et al.* 2006). The perichaetial leaves are erect in both dry and moist conditions and notably hyaline (Figures 2B, C; 5A, C, E), although only the innermost ones in *S. bunyaense* become fully hyaline. In fact, both species of the genus exhibit a gradation whereby the outermost perichaetial leaves show a significant portion of the upper half that is chlorophyllose, whereas in the inner ones the green portion is restricted to the costa and the distal end of the leaf. The areolation of the hyaline tissue constituting these leaves is highly distinctive (Figures 3B, C; 6C), even though it has not been previously underscored (but see Lewinsky 1978). The tissue is composed of trapezoid to rhomboidal elongated cells, always with thin and straight walls. These hyaline cells are strongly differentiated from any basal cells of vegetative leaves, while the cells in the green portions resemble the upper cells of vegetative leaves. To date, a similar feature has never been recorded in any other group of Orthotrichaceae.

Norris & Robinson (1981) highlighted the fact that the strongly modified perichaetial leaves of *Stoneobryum* partly substitute the protective function typically carried out by the calyptra on the immature capsule, which is consequently reduced. This complementary function seems to be most pronounced in *S. bunyaense*, where the inner perichaetial leaves closely adhere to the capsule. In contrast, in *S. mirum*, the perichaetium forms a kind of calyx that completely surrounds the capsule without touching it.

The calyptra, on the other hand, is short, conical and hairy, besides hyaline in the lower part (Figures 2D; 5D). In both *Stoneobryum* species, calyptrae are very similar in shape, but in *S. bunyaense*, it is ephemeral and disintegrates without falling off when the capsules are mature, while in *S. mirum*, the calyptra persists intact and falls off before or upon operculum detachment.

Regarding the sporophyte, relevant common characteristics in both *Stoneobryum* species are found in the seta, as well as in the operculum, peristome, and stomata. The capsules are virtually but not completely sessile, as the seta emerge up to a maximum of 100 µm from the vaginula. The capsule is more or less ovoid, strongly 8-ribbed in the upper half, and abruptly contracted to seta. Stomata are restricted to the neck of the capsule and, clearly cryptopore, appear only partially covered by slightly differentiated exothecial cells (Figure 3G). The operculum is quite distinctive, appearing to lack a rostrum (Goffinet 1997), although it may actually be bluntly apiculate, i.e., mamillate (Figures 5C, D). The virtual absence of a rostrum could be associated with an increased difficulty in calyptra detachment (Goffinet *et al.* 2009). This seems to be the case in *S. bunyaense*, where the calyptra may disintegrate without falling off, but it is not the case in *S. mirum*, where the calyptra easily falls off before the operculum detachment (Figure 5D).

The peristome of both *Stoneobryum* species is very similar (Figures 4A–D; 7), both in architecture and ornamentation: eight pairs of finely ornamented exostome teeth and an endostome of eight linear, faintly striolate segments arising from a well-developed connecting membrane. Until the present study, the presence of the latest structure has not been noted, which has somehow biased the analyses on character evolution in Orthotricheae (Draper *et al.* 2021; Lewinsky-Haapasaari & Hedenäs 1998). However, the endostome connective membrane is tall, formed by several rows of smooth cells (Figure 4A), so that it even protrudes above the mouth of the capsule and is visible when dry (Figures 2E; 4C; 7B).

Many traits are shared between the two species of *Stoneobryum*, and their appearance is also very similar. In fact, Norris & Robinson (1981) highlighted only subtle quantitative traits related to vegetative leaves as distinctive characters between the two species. Their key referred only to the shape of the apex, the end of the costa in the apex, and the transition from the leaf base to the narrower lamina. However, our study reveals the variability of these foliar features in the two analysed species. At the same time, it reveals significant qualitative differences between these two mosses. The most relevant ones refer to the constitution and arrangement of the perichaetial leaves and the composition of the calyptra, which have already been discussed above.

The two species differ also in features of their vaginula, which is completely naked in *S. bunyaense*, versus bearing a distal crown of long hyaline, stiff, and curved hairs in *S. mirum* (Figure 6E). This crown of hairs surrounds the basal part of the capsule, resembling a sort of structured petticoat or crinoline between the capsule and the calyx-like structure formed by the perichaetium. Such structure is not known from any other species, at least within Orthotrichaceae, and hence its function, if any, is ambiguous.

Finally, the two species also differ in their spore ornamentation, although the traits are not easily seen, even in microscopy. In both species, the spores are covered by low and blunt papillae, arranged unevenly over the entire surface, and the distal and proximal faces of the spores are separated by a smooth equatorial ridge—which seems to be made of anastomosed papillae (Figure 4E). However, this unique ornamental pattern among Orthotrichaceae is not equally obvious in the two species. In *S. bunyanense*, the papillae (Figures 3F; 4E) are barely prominent, and the ornamentation of the proximal half consists of papillae arranged radially and is notably less dense than on the distal half; the equatorial ridge is also evident. Conversely, in *S. mirum*, papillae (Figure 6G) are somewhat more prominent, allowing for the curved outline of individual papillae to be discernible, and the difference between the ornamentation of the two portions of the spore is less pronounced, with the equatorial ridge less evident. In light microscopy, the spores of *S. bunyanense* appear more faintly papillose and the ornamentation pattern differs between the two faces of the spores.

The set of distinctive features treated above decisively distinguish *Stoneobryum* from *Sehnemobryum* Lewinsky & Hedenäs (1998: 549), its sister genus in accordance with several phylogenetic reconstructions (Goffinet *et al.*, 2004; Sawicki *et al.*, 2017; Draper *et al.*, 2021), and from *Orthotrichum*, which is the most diverse and heterogeneous genus among the nearest relatives.

Conclusion

Stoneobryum is a highly differentiated genus from a morphological viewpoint. Based on the analysis of its two species and a comparison with closely related genera, it can be concluded that the main characteristics defining and distinguishing *Stoneobryum* are as follows: vegetative leaves crisped when dry, with laminal cells nearly smooth and heteromorphic basal cells differentiated into three longitudinal bands, with the outermost and juxta-costal ones being hyaline; strongly modified perichaetial leaves, mainly formed by hyaline, trapezoid to rhomboidal elongated cells, jointly constituting a perichaetial protective structure for the capsule; calyptra small, covering the distal 1/3 of the capsule, conical, not plicate, hairy; cladocarpous plants; capsule immersed, on a very short seta; stomata cryptoporous, partially covered, restricted to capsule neck; operculum convex, smooth to mamillated; peristome double, with 8 pairs of exostome teeth and 8 endostome linear segments on a tall connecting membrane; isosporous.

The two known species of the genus can be easily distinguished based on characters of the perichaetial leaves, vaginula, calyptra, and spore ornamentation. Both species thrive as epiphytes. While *Stoneobryum bunyaense* is confirmed as an uncommon moss and a local endemic from Bunya Mountains in central-eastern Australia, *S. mirum* is a relatively common and widespread species in eastern South Africa.

The following key summarizes the morphological characters that best allow the distinction of the two species of *Stoneobryum*:

1. Perichaetium forming a calyx-like structure around the capsule, with the inner perichaetial leaves clearly separated from the capsule; vaginula with a crown of apical hairs surrounding the base of the capsule; calyptra detaching intact before the operculum falls .... *S. mirum*.

\- Perichaetium not forming a calyx-like structure around the capsule, with the inner perichaetial leaves closely adhering to the capsule; vaginula naked; calyptra not detaching until the operculum falls and appearing somewhat disintegrated at base in nearly mature capsules .... *S. bunyaense*.

Acknowledgements

We are deeply grateful to Elia San Miguel, Jano Lara, Raúl D. San Román and Nikolay Matanov for their assistance during field campaigns. We are also grateful to the agencies that have provided the permits to collect mosses in protected areas: Ezemvelo KwaZulu-Natal Wildlife Permits Office (Permit OP 38/2022); Eastern Cape Parks & Tourism Agency (Permit RA_0346); NSW National Parks and Wildlife Service (Scientific License SL 100569 and Research Permit RES 100022); Queensland Parks and Wildlife Service (Authority Number P-PTUKI-100327823); Parks Victoria (Permit 100100443). For their help in obtaining these permits, special thanks are due to Marco Duretto and Hervé Sauquet (Herbarium NSW) and Jacques van Rooy (South African National Biodiversity Institute). FL is also grateful to the staff of the National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, whom, in many ways, contributed to make his stay in Australia more comfortable and productive. The authors thank Chris Cargill and the two anonymous reviewers for their constructive comments on previous versions of the manuscript.

The authors acknowledge financial support from the Spanish Research Agency of the Ministry of Science and Innovation (PID2020-115149GB-C21 and PID2020-115149GB-C22). In addition, FL acknowledges the grant awarded by the Spanish Ministry of Universities under the 'Programa de estancias de profesores e investigadores senior en centros extranjeros 2021' (PRX21/00011).

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