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A new riverine species of the liverwort *Fossombronia* (Pelliales, Fossombroniaceae) from Ecuador

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Abstract

A large, light green, mat-forming *Fossombronia* was discovered during explorations in the Río Anzu Reserve in eastern Ecuador in 2008. The plants were found only on scattered limestone boulders along the Río Anzu as it flowed through a narrow limestone gorge. A morphological study of specimens collected in 2008, using a combination of optical and scannning electron microscopy, was conducted. A unique suite of characters of this riverine *Fossombronia*, when compared with those of currently recognized species, supports its recognition as a new species, which is named and described herein as *Fossombronia jostii* Crand.-Stotl. & Gradst. The restriction of this species to a limestone, riverine habitat is shared by *F. texana* and *F. wrightii*, with which it shares some, but not all morphological characters. The impact of a major flooding event on the taxon is discussed, and a key is provided to the six species of *Fossombronia* currently known from Ecuador.

Introduction

The liverwort flora of Ecuador has been much explored since the 19th century explorations of Richard Spruce, yet is still incompletely known (León-Yánez *et al.* 2006, Schäfer-Verwimp *et al.* 2013). Based on his collections from the Ecuadorian Andes, Spruce (1885) named three new species of *Fossombronia* (Raddi 1818), namely, *F. crassifolia* Spruce (1885: 527), *F. ptychophylla* Spruce (1885: 529) [=*F. peruviana* Gottsche & Hampe in Hampe (1854: 555), syn. fide, Crandall-Stotler *et al.* 1999: 76] and *F. tenuifolia* Spruce (1885: 528) [=*F. pusilla* (Linneaus 1753: 1136) (Nees 1838: 319), syn. fide, Freire 2002: 180]. More recently, as part of a specimen-based worldwide monographic study of *Fossombronia* (see http://bryophytes.plant.siu.edu//fossombronia.html for details), Freire (2002) added *F. porphyrorhiza* (Nees 1833: 343) Proskauer (1955: 197) to the flora.

In recent years, bryophyte explorations have been conducted by the second author and L. Jost (LJ), botanist and board member of the Ecominga Foundation, in the Upper Pastaza Watershed of Ecuador. Not only have these new explorations expanded the known liverwort flora of Ecuador (Léon-Yanez *et al.* 2006), but they have also led to the re-discovery of some of the rare taxa orginally collected by Spruce, such as *Myriocolea irrorata* Spruce (1884: 305) (= *Colura irrorata* (Spruce) Heinrichs *et al.* (2013: 58) (Gradstein *et al.* 2004). One area of particular interest within the Pastaza Watershed is the Río Anzu Reserve, which is located on the eastern slopes of the Cordillera Abitagua at an elevation of 1100–1200 m, approximately 10 km N of the town of Mera. A central feature of the Reserve is its limestone substrate. The Reserve includes a narrow limestone gorge, through which flows the Río Anzu (Fig. 1A), and a unique old-growth submontane tropical rainforest that is home to many rare, limestone specialist plants, including the ladyslipper orchid *Phragmipedium pearcei* (Reichenbach 1865: 298) Rauh & Senghas (1975: 62) (Fig. 1B). In 2008 while sampling the bryophytes that cover the boulders along the river's edge (Fig. 1B, 1C), SRG discovered extensive mats of a large, light green *Fossombronia* (Fig. 1D, 2A). Although clearly belonging to the genus *Fossombronia*, these plants did not superficially resemble any of the known species of the genus, except perhaps the high elevation, mire-inhabiting *F. peruviana*, which they resemble in size and semi-aquatic habitat. Determining the taxonomic status of this submontane, riverine population of *Fossombronia* is the objective of this study.

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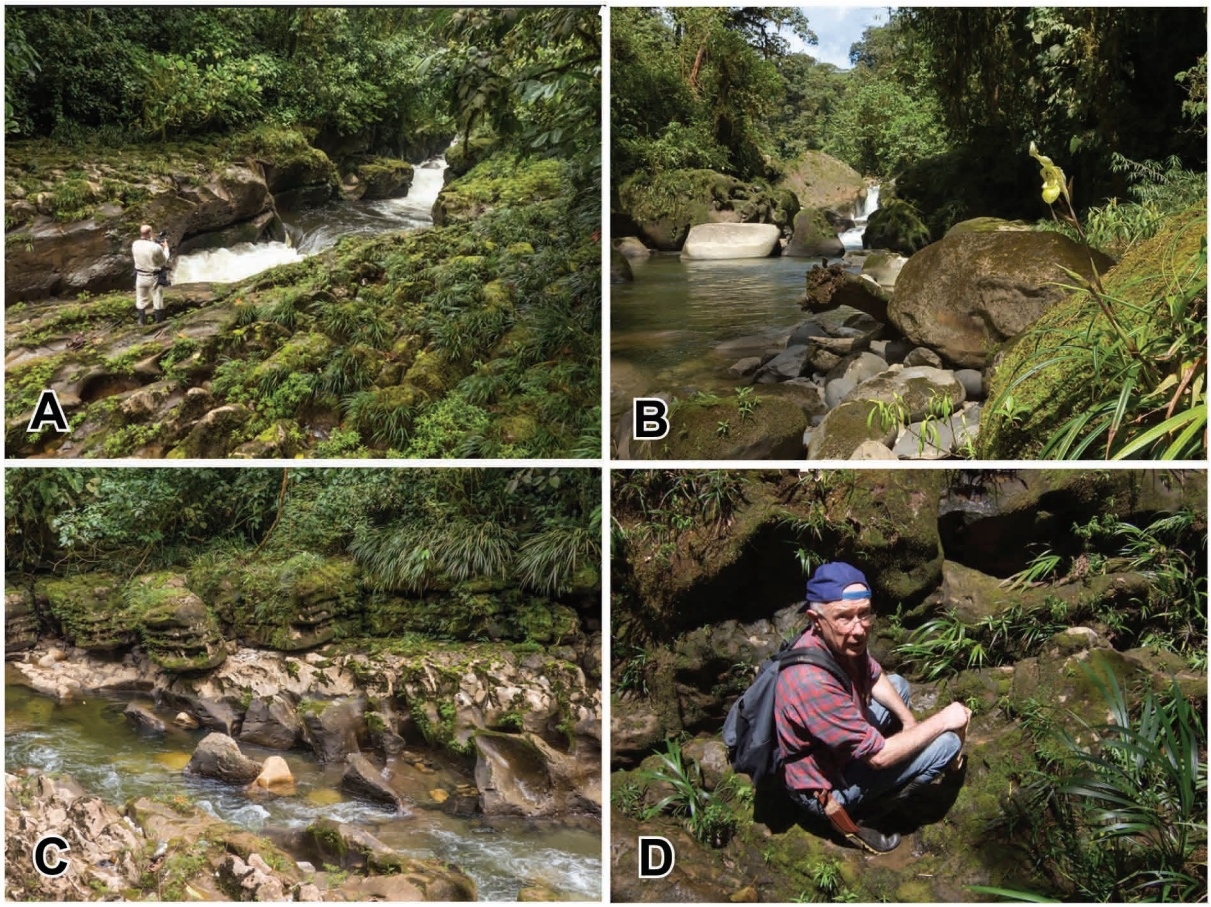

FIGURE 1. The Río Anzu Canyon collecting site in 2008. A and C show the limestone rocks lining the river covered with vegetation and the surrounding forest vegetation; B shows the rare orchid *Phragmipedium pearcii* (Rchb.f.) Rauh & Senghas, on a boulder near the *Fossombronia* collecting site; D shows the second author (SRG) making a collection of the new species. Photos provided by Lou Jost.

Material and Methods

Morphological characters were recorded from dried herbarium samples of the Río Anzu population (*S.R. Gradstein & L. Jost 12126* [GOET, QCA, F]), employing standard, nondestructuve methods of optical microscopy and photography. In addition to preparing a permanent slide mount of spores, elaters and capsule wall in Johnsons Brite floor wax for high magnification study, spores and elaters were removed from a mature, partially-dehisced capsule and placed directly on double-sticky tape on an aluminum Cambridge stub. They were coated with 250 Å gold-palladium in a Denton Desk II sputter-coater, and images were captured on an FEI Quanta 450 Scanning Electron Microscope.

Results

Plants of this Ecuadorian *Fossombronia* are light grass-green, with imbricate, succubously inserted leaves and a prostate habit (Fig. 2A). Shoots range from 2–3 cm long by 2.6–5.0 mm wide, are unbranched, except for an occasional bifurcation, and are firmly attached to their substrate by dense mats of long, dark purple rhizoids that cover the ventral surface of their stems. Leaves are 2- to 3-stratose at the base, but are unistratose for 2/3rds to 3/4th their length, and are oblate, being up to 2.0 mm long near the leaf middle and 4.0 mm wide from acroscopic to basiscopic margin (Fig. 2B). Leaf margins are broadly undulate, and rucked, with 4 or 5 pleats or broad folds that extend to the leaf middle, and leaf cells are uniformly thin-walled, with the cells gradating from rectangular in outline at the leaf base to isodiametric at the leaf margin. Numerous, small, homogeneous oil bodies are found in all cells.

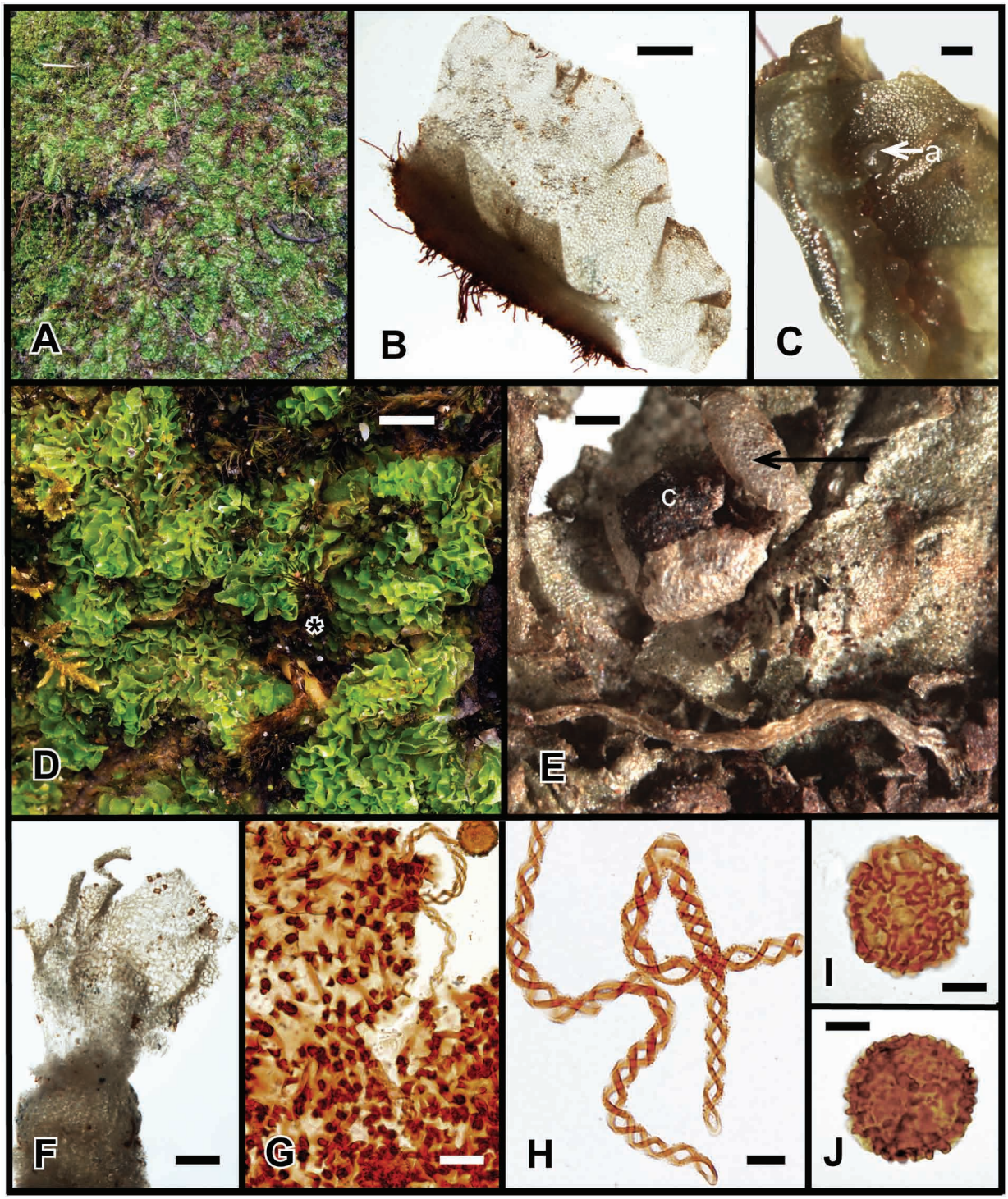

FIGURE 2. Morphological characters of *Fossombronia jostii* Crand.-Stotl. & Gradst., *sp. nov.* A, habit view of a mat of *F. jostii* covering a limestone boulder in the canyon in 2008; B, vegetative leaf, scale bar = 500 µm; C and D, male plants with antheridia, C showing immature antheridia (a) found in 2008 collection, scale bar = 250 µm, and D showing a group of male plants with antheridia (*), after the 2016 flood, scale bar = 2.5 mm; E, portion of a female plant with a mature caulocalyx, at arrow, surrounding a mature but undehisced capsule (c), scale bar = 700 µm; F, portion of a mature caulocalyx, after seta elongation, showing the irregularly toothed mouth, scale bar = 250 µm; G, portion of the inner capsule wall, with an elater and spore, scale bar = 30 µm; H, bispiral elaters, scale bar = 14 µm; I and J, spores, viewed in a compound optical microscope, with I showing the distal face, and J, the proximal face, scale bars = 10 µm. Photos A and D provided by Lou Jost.

The taxon is dioicous and sexually dimorphic, i.e., with the male plants being narrower, with smaller leaves, than the female. Antheridia are borne at the apices of the male shoots, each protected by the dorsally inserted, posterior portion of a developing leaf (Fig. 2C, D). Only a few immature antheridia, which are light green and up to 250 µm

in diameter, were found in the original 2008 collections, but in a recent return to the area, a small population of male plants, with numerous immature green and mature yellow-orange antheridia, was photographed by LJ (Fig. 2D). In contrast, no plants bearing unfertilized archegonia have ever been observed although a few very young sporophytes and plants with mature, fully dehisced capsules on elongated setae, were present in the original collection, along with seemingly mature, spheroidal capsules just emerging from their caulocalyces. Mature sporophytes occur posterior to the shoot apex on the dorsal side of the stem between two mature leaves (Fig. 2E). Although there is only a single mature sporophyte per shoot, their development does not appear to halt further growth of the stem since immature leaves are found anterior to them. The caulocalyx is nonstipitate, broadly campanulate and deeply divided into three large lobes that fold inwards over the capsule as it matures. Margins of the caulocalyx lobes are irregularly toothed (Fig. 2E, F).

Setae are large, up to 13 cells in diameter and 1.5 mm when elongated. Capsules are dark brown to black, spheroidal, 1.2–1.4 mm in diameter, with walls comprised of two cell layers. The outer wall cells are hyaline, thin-walled and collapsed at the time of capsule dehiscence. The inner wall cells are short rectangular to quadrate and possess slightly reddish brown, I-type thickenings on all radial walls (2G). Elaters are variable in length, but with most being 190–210 µm long and 7–9 µm in width. They possess two intertwined, brown thickening bands throughout most of their length, but can have three such bands in the middle (Fig. 2G, H). Spores are 28–32 µm in diameter across the distal face, 24–26 µm in polar diameter, and light to medium brown, with irregularly arranged rounded ridges, or vermiculi, on the distal face and scattered verrucae on the proximal face (Fig. 2I, J & Fig. 3). The distal face vermiculi are 1.9–2.2 µm high and 0.9–1.0 µm wide, and give the spore margin a tuberculate appearance (Fig. 3A). The proximal surface is marked centrally by a triradiate ridge that is ornamented with a few large verrucae, up to 6 µm in height, and three flattened, triangular faces that bear scattered small verrucae, less than 2 µm high (Fig. 3B).

No type of asexual reproductive or perennating structure was observed within the collections; i.e., tubers and gemmae are absent.

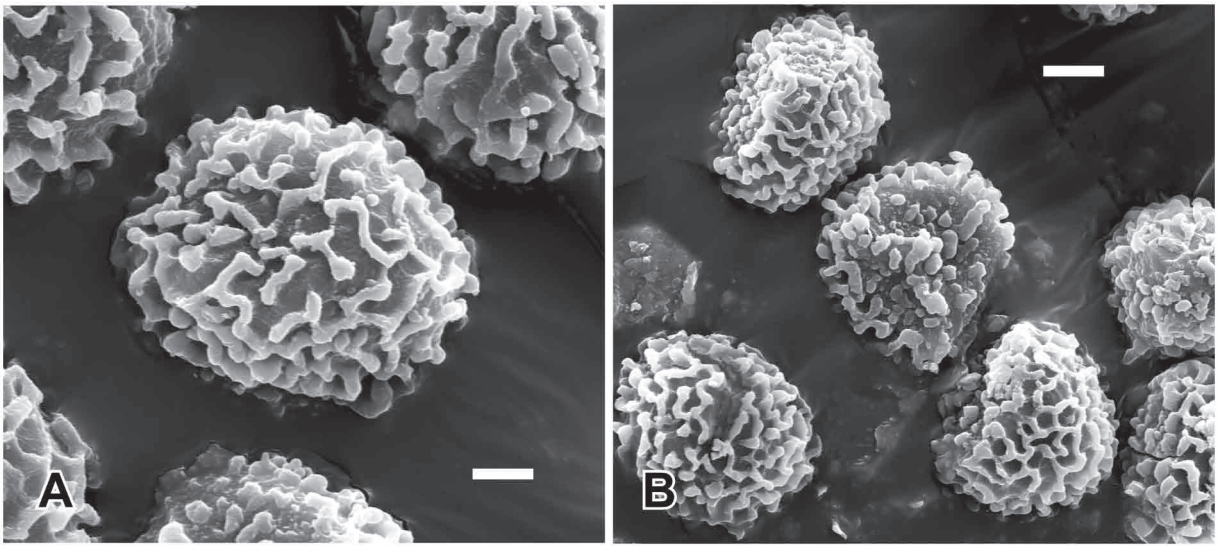

FIGURE 3. Spores, viewed in SEM. A, showing the irregular vermiculi of the distal face, scale bar = 5 µm, and B showing proximal (center spore) and lateral (upper right spore) views, scale bar = 7 µm.

Discussion

Most of the described species of *Fossombronia* grow on exposed moist, often loamy soil, frequently in somewhat disturbed habitats, such as banks along roadsides or small streams, or in pockets of soil in somewhat grassy or rocky habitats. Much of the species diversity in fact occurs in habitats with seasonal dry periods, during which the taxon survives either as spores or by producing fleshy dormant tubers. In contrast, there are a few species that occur in consistently wet, even semi-aquatic habitats, including *F. peruviana* from the high elevation parámos and punas of the Andes and *F. australis* Mitten (1876: 73) from low elevation wetlands in Australia, New Zealand and the Subantarctic Kerguelan and Prince Edward Islands. There are also two species, namely, *F. texana* Lindberg (1875: 533) and *F. wrightii* Austin (1876: 9), that form mats over calcareous boulders in or next to rivers, where they are frequently

inundated, a habitat very like that occupied by the Río Anzu populations. Another riverine species, *F. mylioides* Inoue (1973: 296) is endemic to Iriomote Island, Japan, where it grows on open boulders covered with sandy soil, along the Urauchi and Nakama Rivers (Krayesky *et al.* 2005, Higuchi 2016). Of these riverine species, *F. texana* is the more widespread, occurring in scattered locations in the Interior Highlands of Oklahoma, Arkansas and Missouri, throughout the Hill Country of central Texas and south into Mexico and the Caribbean Islands; to date, *F. wrightii* is known only from its type collection made by C. Wright in Cuba (Freire & Stotler 2007), and *F. mylioides* is restricted to the Ryukyu Islands.

The Río Anzu population of *Fossombronia* differs morphologically from all currently recognized species of the genus, including the high elevation Andean species, *F. peruviana,* and both New World riverine species. It resembles *F. peruviana* in its large size, large, deeply pleated, oblate leaves, and its dioicous sexuality, but differs as follows: the caulocalyx is sessile and broadly campanulate as compared to the long stipitate, urnulate caulocalyx of *F. peruviana*; capsules are spheroidal, with nodular inner wall thickenings, in contrast to ovoidal, with semiannular inner wall thickenings in *F. peruviana*; and spores are smaller than those of *F. peruviana* and have a totally different spore wall architecture (see Crandall-Stotler *et al*. 1999 for characters of *F. peruviana*). *Fossombronia texana* can approach the Río Anzu population in size, but has leaves that are longer than wide, is monoicous, and has larger spores that are distally ornamented with thin lamellae and proximally are without a trilete marking (Bray 2001; http://bryophytes.plant.siu.edu/ftexana.html). Like *F. texana*, *F. mylioides* has oblong to quadrate, never oblate, leaves, is monoicous, and has spores that are up to 46 µm in diameter and are distally cristate to lamellate. The major characters differentiating *F. wrightii* from the Río Anzu population are its sub-quadrate leaf shape, fleshy apical tubers, and very large (55–60 µm), dark reddish brown spores; however, this species is dioicous, has a sessile caulocalyx, has nodular inner capsule wall thickenings, and a densely vermiculate somewhat areolate distal and verrucate proximal spore wall architecture, with a distinct, proximal trilete marking (Freire 2002; http://bryophytes.plant.siu.edu/fwrightii.html). Overall, the characters of *F. wrightii* could suggest a distant relationship with the Río Anzu plants, but not a species level identity with them. The suite of morphological characters expressed by this *Fossombronia* from the Río Anzu Reserve does not occur in any other named species of the genus, supporting its recognition as a new species.

Taxonomy

Fossombronia jostii Crand.-Stotl. & Gradst. *spec. nov.*

Plants robust, light grass-green, without secondary pigments in stems or leaves. Leaves broadly oblate, up to twice as wide as long, with cells of the leaf middle, 40-70 µm long and 35-40 µm wide. Dioicous, with male plants smaller than females. Caulocalyces subterminal, sessile, broadly campanulate, with the mouth incurved. Capsules spheroidal. Spores 28–32 µm in diameter, light to medium brown, with the outer spore wall irregularly vermiculate, without areoles. Tubers lacking.

Type:—ECUADOR. Pastaza Province: Río Anzu Reserve, ca. 10 km N of Mera, deep gorge in primary and old secondary rainforest reserve, ca. 1100 m, forming conspicuous, light green mats on moist, periodically inundated limestone rock in riverbed, 19 September 2008, *S.R. Gradstein & L. Jost 12126* ((holotype GOET! isotypes QCA! F(ABSH)!).

The new species is named in honor of Lou Jost, orchid specialist and conservationist at Baños, Ecuador, who accompanied the second author in the field, led him to the site where the new species was found, and has provided much of the photographic documentation of the species in its natural habitat.

Fossombronia jostii forms extensive mats on several limestone boulders along the river and is easily recognized in the field by the grass-green color of both stems and leaves, with no development of reddish-purple pigmentation, as is common in other Latin American species. Plants are large, to 5 mm in width, with elongate, fleshy stems and imbricate, planate, succubous leaves that are mostly unistratose, becoming 2- to (3)-stratose at the base. Leaf margins are unlobed, broadly undulate and pleated, with the dorsal insertion extending to the midline of the stem. Leaf cells are leptodermous and gradate from isodiametric, 25–30 µm in diameter along the margin, to larger, rectangular cells, 40–50 µm by 60–100 µm, at the base. The ventral side of the stems is densely covered with long, purple to reddish-purple rhizoids.

The species is sexually dioicous, with male plants 2.6–3.0 µm wide, i.e., slightly smaller than the females. Mature antheridia are yellow to orange and clustered near the shoot apex; details of archegonial structure and distribution are unknown. Sporophytes develop within a broadly campanulate, nonstipitate caulocalyx, the mouth of which is deeply lobed and inflexed over the expanding spheroidal capsule. Spores are smaller than those of most species of

Fossombronia, are brown, are distinctly ornamented with anastomosing rounded ridges, or vermiculi, on the distal face and have a defined trilete mark on the proximal face.

In addition to its unique suite of characters, *Fossombronia jostii* also occupies a rare habitat for the genus. With the addition of *F. jostii*, three of the 80 known species of *Fossombronia* have been collected only from limestone habitats in and along streams and rivers. During heavy rains, these sites may be inundated by swift-flowing water that can dislodge many of the plants growing on them. In fact, this type of disturbance impacted the Río Anzu site when heavy rains in the area caused extreme flooding along the river (Fig. 4). The walls of the canyon and most of the rocks along the river were denuded of much of their vegetation (Fig. 4A, B), and near-by trees were dislodged by the force of the water. Although the extensive mats of *F. jostii* were gone, on several boulders new growth was visible from the shoot apices of otherwise dead plants (Fig. 4C, D), including a population of males that were already producing antheridia (2C). Despite the extreme disturbance the flooding caused, this species is, nonetheless, able to persist in this tropical, submontane riverine system. Further exploration is required to determine whether *F. jostii* is restricted to the Río Anzu or is more widespread, also occurring in other limestone-based riverine habitats in Latin America.

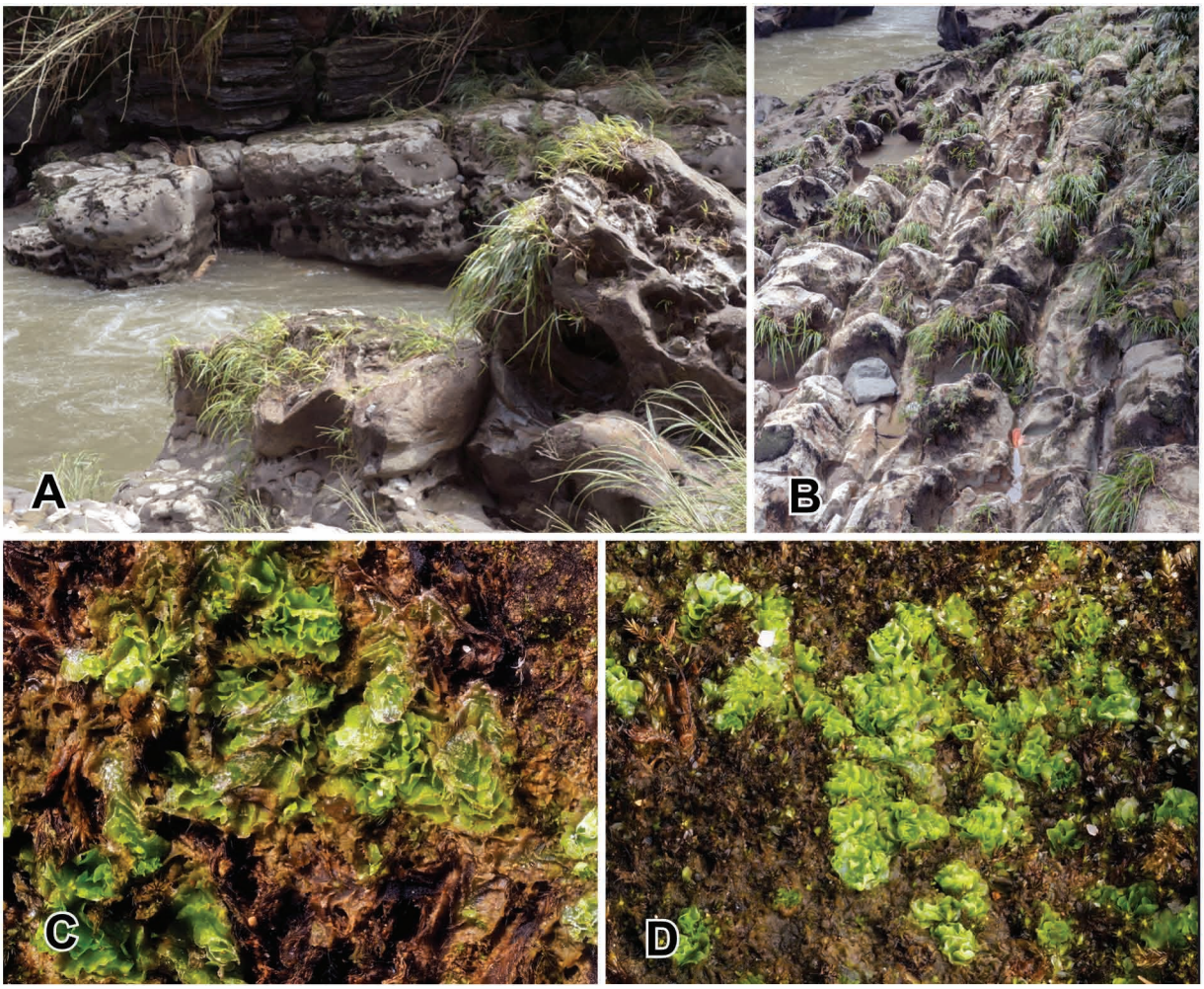

FIGURE 4. The Río Anzu canyon site after a 2016 flood. A and B show rocks along the river almost denuded of vegetation; C and D show *Fossombronia jostii* regenerating from the apices of otherwise dead plants (C), with new growth spreading to form new mats (D). Photos provided by Lou Jost.

Key to the species of *Fossombronia* from Ecuador

With the discovery of *F. jostii* in Pastaza Province, six species of *Fossombronia* are currently known to occur in Ecuador, namely, *F. crassifolia*, *F. fernandeziensis, F. jostii*, *F. peruviana*, *F. porphyrorhiza* and *F. pusilla*. In contrast to the list in León-Yánez *et al.* (2006), our list excludes *Fossombronia lophoclada* Spruce (1885: 529), which Spruce described from Peru, not Ecuador, and adds *F. fernandeziensis,* based on the following collections made by the second author: Chimborazo Province: road to Chunchi, 2350 m, *Gradstein et al. 3362* [GOET]; and Pichincha Province: old road from Quito to St. Domingo, between Chillogallo and San Juan, 3450 m, *Gradstein et al. 6717* [GOET, F(ABSH)]. These six species may be keyed out as follows:

1. Plants large, up to 6 mm wide, growing in very wet habitats, periodically submerged in mires, streams or rivers. Leaves patent to suberect, twice as wide as long, margins entire, undulate, with 4 to 6 broad pleats (rarely planate). Seta more than 12 cells in diameter. Dioicous 2
- Plants smaller, 1.5-4 mm wide, growing on moist soil, never submerged. Leaves horizontal to patent (if suberect to erect, with the leaf base 4 to 5 cell layers thick), never twice as wide as long, with the margins entire or lobed, not deeply pleated. Seta fewer than 10 cells in diameter. Monoicous 3
2. Plants green, with reddish or brownish pigmentation in both stems and leaves. Midleaf cells (50–)70–120 × 40–60 µm. Capsules longer than wide. Spores (31–)35–39 µm in diameter, distal surface lamellate-reticulate, with incomplete areoles. In páramo and puna, above 3000 m..... *F. peruviana*
- Plants light grass-green, lacking reddish or brownish pigmentation in stems and leaves. Midleaf cells 40–70 × 35–40 µm. Capsules spheroidal. Spores 28–32 µm, distal face with irregularly arranged, rounded vermiculi, without areolae. On limestone rocks in river, 1100 m ..... *F. jostii*
3. Spore 36–42 µm, distal surface regularly reticulate, with 3 to 5 areolae across the diameter. Tubers absent ..... *F. porphyrorhiza*
- Spores 40–58(60) µm, distal face lamellate. Tubers present or absent 4
4. Leaves longer than wide, planate. Leaf margin entire, with a border of elongate cells. Apical tubers present. Spore distal face with 16 to 20 parallel lamellae ..... *F. fernandeziensis*
- Leaves wider than long, undulate or crispate. Leaf margin entire or toothed, without border of elongate cells. Tubers absent. Spore distal face with 10 to 12 lamellae 5
5. Leaves patent, with the leaf base to 3 cell layers thick, with the margins irregularly dentate, sometimes lobed. Spore distal face with lamellae anastomosing, sometimes forming up to three central areolae; elaters with 2(3) loosely coiled, spiral thickening bands ..... *F. pusilla*
- Leaves suberect to erect, crispate, with the leaf base 4 to 5 cell layers thick with the margins entire. Spore distal face with lamellae never forming central areolae; elaters with 3, 4 (5) tightly coiled, spiral thickening bands ..... *F. crassifolia*

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