FOSSOMBRONIA PSEUDOINTESTINALIS (FOSSOMBRONIAEAE, MARCHANTIOPHYTA), A NEW SPECIES FROM SOUTHERN AUSTRALIA

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FOSSOMBRONIA PSEUDOINTESTINALIS (FOSSOMBRONIAEAE, MARCHANTIOPHYTA) – НОВЫЙ ВИД ИЗ ЮЖНОЙ АВСТРАЛИИ

INTRODUCTION

The family Fossombroniaceae Hazsl. comprises one genus, Fossombronia Raddi. Fossombronia is defined by the leafy appearance of the plants (Fig. 1A), typically purplish-red rhizoids (Fig. 1B), although hyaline or brownish rhizoids also occur, naked gametangia dispersed along the stem or protected by perigonal scales (Fig 1C, D, E) and sporophytes enclosed by a shoot calyptra and caulocalyx (Fig. 1F, G, H). Söderström et al. (2015) accepted 66 species in the genus with another 16 species of uncertain taxonomic status. Species diversity is greatest in Australia (29 species: pers. obs.) and South Africa (20 species: Perold, 1999).

Like many Riccia L. species, Fossombronia is a common liverwort of compacted soil in Australia, particularly across southern Australia (Fig. 2A), occurring in woodlands, forests and disturbed sites such as roadsides. Spore characters have traditionally been particularly important in distinguishing amongst species (Schuster, 1992; Milner et al., 2011), but more recently gametophyte characters have increasingly been found to be useful (Perold, 1997; Cargill, 2001; Krayesky et al., 2005). Very few species, however, can be reliably identified from characters of the gametophyte alone, particularly Australian species. Several species may be morphologically similar at the gametophyte stage yet have very distinctive spores (Milner et al., 2011).

According to Australasian Virtual Herbarium (AVH) records accessed 6th Jan 2021 & 23rd May 2021; https://avh.chah.org.au/, twenty species of Fossombronia have been recorded from the southern Australian state of New South Wales. Early collections were made near Sydney in the late 1800’s and early 1900’s by T. Whitelegge, W. Forsyth and E. Cheel in the greater Sydney region and later in the early 1900’s by Rev. W.W. Watts in regional NSW. More recently, many more collections have been made along the east coast and well into central NSW, but not beyond the western regions in the south (Interim Biogeographic Regionalisation for Australia (IBRA) Version 7 2012. https://www.environment.gov.au/system/files/pages/5b3d2d31-2355-4b60-820c-e370572b2520/files/ibra-regions.pdf) or beyond Cobar in the central west (IBRA Cobar Penplain region) or Bourke on the Darling River (IBRA Mulga Lands region) (except for two outliers, one collection at Wentworth in the far southwest of the state and one at Tibooburra in the far northwest of the state). Almost half of the state is under-explored for this genus.

A collecting trip by Australian National Herbarium associates, Dr Rosemary Purdie and Murray Fagg to the Bendick Murrell National Park (Fig. 2C, map from ALA spatial portal via AVH, accessed 13th June 2021) near the small township of Greenthorpe in the IBRA NSW South Western Slopes region of NSW resulted in the discovery...
Fig. 1. Images of characteristic structures of *Fossombronia*. A. Leaf-like lobes of thallus of gametophyte. B. Reddish-purple rhizoids of gametophyte. C. Perigonial scales associated with antheridia of a male thallus. D. Antheridia subtended by perigonial scales. E. Naked archegonia of female thallus. F & G. Fertile plants with cup-shaped caulocalyces at the bases of the capsules. H. SEM of the campanulate shaped caulocalyx. A. *Fossombronia papillata* D.C.Cargill 1280 (CANB); B. *F. sp.* culture D.C.Cargill 566; C. *F. angulosa* J.Paton s.n. (ABSH); D. *F. capensis* var. *capensis* S.Arnell 1376 (S); E. *F. angulosa* J.Paton s.n. (ABSH); F. *F. sp.* R.W.Purdie 12091 (CANB); G. *F. vermiculata* D.C.Cargill 789; G. *F. capensis* var. *capensis* S.Arnell 1876 [sic 1376] (S). Photo F. taken by Murray Fagg, photo G taken by Bruce A. Fuhrer, all other photos taken by D.C.Cargill.
of a fruiting Fossombronia superficially similar to the common Fossombronia intestinalis Taylor. However, based on both vegetative and spore characters, this material seems to represent a new taxon, described here as Fossombronia pseudointestinalis Cargill.

This paper celebrates the 100th year of the birth of Prof. Rudolph M. Schuster, whose landmark publications on the liverworts of the ‘antipodes’ and in particular the 6th volume of his prodigious six volume The Hepaticae and Anthocerotae of North America very much influenced my own work through the years on both the hornworts and the complex thalloid liverworts as well as Fossombronia.

MATERIALS AND METHODS

Live plants were examined and measured for all morphological characters using Leitz compound and dissecting microscopes. All quantitative characters were based on measurements taken on multiple plants to record the range of variation. Where capsules were present, spores were mounted in water on microscope slides for light microscopy (LM) or on double sided sticky tape on aluminum stubs, gold-coated with an EmiTech K550X Sputter Coater and viewed using a Zeiss EVO LS 15 Environmental SEM. The Royal Horticultural Society Colour Chart (RHSCC)1 was used to describe colours of whole plants and spores. In situ images of the plants were taken by Murray Fagg with a Canon EOS Mirrorless camera with a Canon EF-M 28 mm f/3.5 macros IS STM lens. Light micrographs were obtained with a Nikon Coolpix 5000 digital camera. All line drawings were made using drawing tube attachments to both microscopes.

TAXONOMIC TREATMENT

Fossombronia pseudointestinalis Cargill, sp. nov.
Figs. 3–9

Diagnosis. Plants are vegetatively similar to Fossombronia intestinalis with which it shares concave overlapping leaves, giving the plants a tube-like appearance. Fossombronia pseudointestinalis, however, is a brighter green often with fuchsia tinges along margins compared to the pale green frequently seen in F. intestinalis. Fossombronia intestinalis plants are also broader and smaller than those of F. pseudointestinalis. Distally, the spores of F. pseudointestinalis have thick vermiculate bands and nodules, no reticulate patterning or areolae and with large, thick verrucae on the proximal face. Spores of F. intestinalis are reticulate distally, the areolae bordered by tall thin lamellae and with patterns of almost flat irregularly shaped verrucae and lamellae over the proximal face.


Plants observed in nature.

Description. Plants in nature gregarious, forming small, scattered patches, bright green (RHS 144A, yellow-green group and with fuchsia tinges RHS 59B in female plants), prostrate, up to 7.0 mm long, 1.5–2.5 mm wide, 1.3–2.5 mm in height; sparingly branched, unbranched or 1x furcate, with branches ventral-lateral. Leaves closely imbricate, erect, often with shallow ribs or crests or less frequently, large leaf-like lobes, protruding out perpendicular to main leaf, not running the length of the leaf, variable in length, or without crests, concave, inserted longitudinally, succubous with antical margin decurrent on some leaves in male plants, oblate to quadrate in female plants, oblate to quadrate to lingulate in male plants, 0.8–1.95 mm long × 0.6–3.1 mm wide, 0.45–
Fig. 3. Fossombronia pseudointestinalis. A–B. Plants of *F. pseudointestinalis* in situ. C. Dorsal view of vegetative plant showing the tube-like habit of the species. D–E. Whole fertile plants showing the pinkish tinge of the margins of the caulocalyx and the dark brown rhizoids. Scale divisions in B, D and E are 1 mm. Images all taken from *RW Purdie 12052*. Photos A and B taken by Murray Fagg; all other photos taken by D.C. Cargill.
Fossombronia pseudointestinalis, a new species from southern Australia

Fig. 4. Leaves of Fossombronia pseudointestinalis. A. A large lobed, oblate leaf typical of the species. B. Single leaf. C. – D. Leaf lobes. E. Crest on the distal face of a ‘compound’ leaf. F. Mid-leaf cells containing chloroplasts and oil bodies. Images all taken from RW Purdie 12052. All photos taken by D.C. Cargill.
Fig. 5. *Fossombronia pseudointestinalis* (from holotype). A. Cross section through the stem of a plant showing an archegonium. B. Antheridium. C. A naked, unfertilized archegonium stained with toluidine blue. D. – E. Caulocalyces showing the pinkish pigmented and highly dissected margins. F. A stipitate caulocalyx (at arrow). G. Capsule wall with banded thickenings within the cells. Elaters in the bottom righthand corner. All photos taken by D.C. Cargill.
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Fig. 6. SEM & LM images of spores of *F. pseudointestinalis* (from holotype). A. Group of spores and elaters. B. Three spores of a tetrad showing the hemispherical shape of spores in equatorial view. C. Distal view of spore. D. Proximal view of spore. E. & F. LM images of distal and proximal view of spores. All SEM photos taken by D.C. Cargill.
2.8 mm wide at leaf insertion; margins shallowly lobed, with lobe shape variable; margins entire to irregularly dentate; leaf apex rounded or truncate; median leaf cells polygonal isodiametric to elongate, 32.5–137.5 μm long × 20–62.5 μm wide, without conspicuous trigones; numerous segmented oil bodies in all cells; marginal cells undifferentiated along the apex of leaves, becoming elongated along the sides. Stems ovoid to plano-convex; 400–1070 μm wide × 500–1180 μm high. Ventral scales not observed. Rhizoids thick along ventral surface and flanks of stem, brown. Tubers absent.

Dioicous. Male plants similar in size to female plants. Antheridia clustered on dorsal surface posteriorly in between leaves; ovoid, 237.5–350 × 225–335 μm. Perigonal scales absent. Archegonia only seen clumped around bases of caulicycles. Caulicycles 1 to 6 per shoot, dorsal, campanulate to urceolate, with 1 or 2 sinuses; with the height less than the plant width (1.3–2.15 mm high), extending slightly higher than the plant leaves; 1.3–1.6 mm across at the widest point, sessile to shortly stipitate; surface with a number of small crests or scale-like projections on the external surface or with several narrow ribs around the circumference of the caulicyclo; caulicly margin irregularly lobed to ragged in appearance, frequently with reddish pigmentation; deeply and irregularly lobed; mouth erect to slightly incurved. Sporophytes emergent, with mature setae 3.2–7.75 mm long. Capsules spheroidal to slightly wider than high, due to being
Fig. 8. Female plants of *Fossombronia pseudointestinalis* (from holotype). A. – B. Whole fertile plants. C1. – C2. Caulocalyces with emergent sporophytes with the caulocalyx opened and flattened out to show the margins. D. Leaves. E. Marginal cells of a leaf with a single slime papilla. F. Mid-leaf cells. Illustrations by D.C. Cargill.
Fig. 9. Male plants of *Fossombronia pseudointestinalis* (from holotype). A, C. Side view of entire plant. B, D. Dorsal view showing the antheridia interposed between the leaves. E. Leaves. Illustrations by D.C. Cargill.
slightly depressed at the apex; 1.0–1.1 mm in diameter, dark brown (RHS 200A brown group); epidermal cells hyaline; inner capsule wall cells with deep brown, I-type, J-type and U-type thickenings. Spores more or less tetrahedral in equatorial view and spheroidal in polar view, 32.5–45 μm diameter, dark brown, disassociated when mature; distal surface with short thick verruculate bands and nodules, with 17–24 projections around margin, length of projections varying between populations, 2.5 μm long, 2.5–5.0 μm wide at base; micro-ornamentation of intervening surface with low verrucae or papillae; proximal surface with a pattern of large irregular verruculae and papillae; triradiate ridge more or less distinct; equatorial wing absent. Elaters abundant, elongate, infrequently short, 87.5–200 μm long, 7.5–12.5 (–17.5) μm wide, occasionally to frequently branched, (1-) 2- or 3-spiraled, with spirals moderately to loosely coiled; outer wall hyaline, spirals dark reddish brown, with surface smooth. Gemmae lacking.

Etymology. Named for the morphological similarity of the gametophyte to that of Fossombronia intestinalis.

Distribution and habitat. Known only from the type locality, growing in Callitris endlicheri low open forest with scattered emergent Eucalyptus.

Conservation status. This species has not been formally evaluated and is so far only known to occur within Bendick Murrell National Park, where it has been recorded from only one site. According to IUCN criteria (IUCN 2019) it would be listed as “Not Evaluated”.

Discussion

The tube-like habit of this species is not unusual amongst Australian Fossombronia taxa (Fig. 3B, 7B). A relatively common Australian endemic showing this morphotype is Fossombronia intestinalis (Fig. 7A – C), one of the few Australian Fossombronia species that can be identified from vegetative characters from all other Fossombronia species. In comparison of plants of Fossombronia intestinalis and F. pseudointestinalis, the leaves are unusual in both species: some leaves are much broader than high and multi-lobed (Fig. 4A, 8D, 9E), with some individual leaves bearing several vertical crests or ribs or in some cases large leaf-like lobes, demarcating the individual marginal lobes of the large leaf. These crests are seen in both species but are usually relatively short in F. pseudointestinalis vs those in F. intestinalis which run the full length of the leaves. The crests appear to develop as the leaf matures and are not seen in young developing and juvenile leaves. Also, the margins of the leaves of F. pseudointestinalis are generally entire vs those of F. intestinalis which are always toothed with teeth ranging in size from one to 8 cells in length capped by a slime papilla. Both the leaves and caulocalyces of female plants are also frequently tinged a dark pinkish colour in F. pseudointestinalis (Fig. 5D – F), vs pale green to whitish green in F. intestinalis (Fig. 7A, C). Rhizoid colour also differs between the two species, with F. intestinalis typically red wine-coloured vs dark brown in F. pseudointestinalis (Fig. 3D, E). This rhizoid colour is an easy character to separate the two species and could be used to identify infertile herbarium specimens which look similar to F. pseudointestinalis.

The height and morphology of the caulocalyx also differs between the two species, extending slightly above the leaves in F. pseudointestinalis, but at the same height as the leaves in F. intestinalis. In the latter, the caulocalyx is not such a distinct structure and appears more like two or more slightly modified, partially fused leaves which surround the calyptra of the sporophyte vs a distinctly campanulate shaped structure seen in F. pseudointestinalis. Capsule wall thickenings differ between the two species, with those of F. intestinalis being mainly annular and semi-annular vs 1-, J- and U-shaped and annular thickenings frequently seen in the capsule walls of F. pseudointestinalis. Spore wall architecture also clearly distinguishes the two species. Fossombronia pseudointestinalis displays a verruculate pattern distally of long and short thick muri and nodules and a pattern of papillae and verruculae proximally, with a more or less distinct triradiate mark (Fig. 6), vs a loose reticulate pattern of taller thinner lamellae bordering complete or incomplete areolae forming a maze-like pattern across the distal face and a covering of almost flat verruculae and short, irregular shaped lamellae over the proximal face for F. intestinalis. Elaters are similar between the two species, both have relatively long, narrow elaters (F. intestinalis elaters are 150-225 × 7.5–12.5 μm vs 87.5–200 × 7.5–12.5 (–17.5) μm for F. pseudointestinalis), however, the number of strands making up the thickenings does differ. Fossombronia intestinalis has both 2- and 3-spiralled elaters vs the majority of 2-spiralled for F. pseudointestinalis with a few 3-spiralled.

Other species of Australian Fossombronia may not share similar gametophyte morphologies but instead share similar spore patterns. Fossombronia cerebriformis, (Scott & Pike, 1984) F. hewsoniae (Scott & Pike, 1987) and F. scrobiculata (Scott & Pike, 1984) all share a distal pattern consisting of verruculate-like bands and nodules. The Fossombronia cerebriformis pattern differs in the width of the bands, which are thinner (0.83–3.35 μm wide) and more numerous vs the thicker bands (1.63–5.74 μm wide) of F. pseudointestinalis, while those of F. hewsoniae and F. scrobiculata are also thick (2.13–6.44 μm; 1.25–6.78 μm respectively). All share a similar spore colour – dark brown to almost black, except F. scrobiculata spores which are always dark maroon. The spores of F. pseudointestinalis are relatively small (32–45 μm) vs the large spores of the other three species: F. cerebriformis (51–90 μm), F. hewsoniae (52–72 μm) and F. scrobiculata (45–67 μm) in diameter. The most similar in distal ornamentation to F. pseudointestinalis are the spores of F. hewsoniae. Both have thick rounded bands, however, this pattern is continued on the proximal face of F.
hewsoniae but not *F. pseudointestinalis*. The pattern instead is of nodules and short bands with a spidery micro-ornamentation of thin bands radiating from the base of the thicker bands and nodules (Fig. 6D) along with a distinct triradiate mark, absent in *F. hewsoniae*.

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