BOTANIC GARDENS OF SYDNEY

Telopea

Journal of Plant Systematics

ISSN 2200-4025 (Online)

The fruiting body of *Treubia tasmanica* (Marchantiophyta: Treubiaceae)

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Abstract

Sporophytes of *Treubia tasmanica* R.M.Schust. & G.A.M.Scott, newly discovered in 2021, differ in several ways from what is generally accepted as 'normal' for liverworts. The seta is chlorophyllose, slow growing and persists after spore dispersal. While in growth the sporophyte is positively phototropic, and responsive to changes in light orientation on timescales of hours. There is some evidence the seta goes into senescence before expiring. The opened capsule valves are capable of closing in adverse weather and subsequently re-opening under dry conditions. These discoveries call for some revision of the assumption that all liverwort capsule valves are mere passive actors in the life of sporophytes once dehisced.

Introduction

The small genus *Treubia* K.I.Goebel (Marchantiophyta: Treubiaceae) includes around 10 species and is represented in Tasmania by two: *T. lacunosa* (Colenso) Prosk., and *T. tasmanica* R.M.Schust. & G.A.M.Scott. Meagher (2008) stated that *Treubia tasmanica* was previously known also from Victoria but may now be confined to Tasmania since the two formerly known populations in Victoria were destroyed some years ago by earthworks. However, he reported the presence of populations in the West Tyers in 2015, so the species may still be extant in that state (D. Meagher, pers. comm.). In Tasmania the species is apparently widespread near Lake St. Clair, at the southern end of the Cradle Mountain – Lake St. Clair National Park (D. Meagher, pers. comm.), but there are remnant populations elsewhere on the island, including on the Blue Tier in the State's northeast.

Meagher and Fuhrer (2003) wrote: 'As far as we know, sporophytes have never been found.' However, fruiting specimens have since been collected by Neville Scarlett in the West Tyers site in 2006 (D.C.Cargill, pers. comm.). Collections in the Tasmanian Herbarium (HO) do not include sporophytes. The species has now been collected with sporophytes on the Blue Tier. A detailed description and notes are appended here.

Schuster and Scott (1969) extensively described the gametophyte of *T. tasmanica*. This paper mainly describes the novel finding and development of the unusual sporophyte.

Thekathyil T (2024) The fruiting body of *Treubia tasmanica* (Marchantiophyta: Treubiaceae). *Telopea* 27: 85–99.
doi:10.7751/telopea17631

Received: 6 August 2023
Accepted: 23 January 2024
Published: 20 June 2024

Materials and methods

Observations with photographic records were made on the same population over three seasons: there were three records between 11–17 November 2021, 54 records between 21 September and 24 November 2022 and 10 records between 8 May and 19 July 2023. Time lapse images taken over that period demonstrate previously unrecorded observations of sporophyte development in this species.

A specimen collected in mid-November of 2021 included several plants sporting three still erect setae with dehisced capsules and a single developing sporophyte. The plants were growing on a well-trodden track over plant litter in semi-permanent shade in degraded cool-temperate rainforest (Fig. 1). Accompanying bryophytes were *Chiloscyphus* sp., *Gackstroemia weindorferi* (Herzog) Grolle, *Lepidozia* sp., and *Lepicolea scolopendra* (Hook.) Dumort. ex Trevis. The specimen was collected on a tray and kept under cover in the shade for drying as a herbarium specimen. No attempt was made to keep it alive, but the substrate composed of organic debris was sufficiently moist to keep the plants alive for several days and permitted some observation of growth before desiccating. Glenny *et al*. (2015) state 'In *Treubia*, the mucilage is exuded from clefts in the ventral thallus and swells dramatically when it absorbs water. It may function for water storage …'. Although the authors had not included *T. tasmanica* in their study, this phenomenon has also been observed in the species under discussion and may further explain why the specimen was able to remain turgid for several days under dry conditions.

Fig. 1. *Treubia tasmanica* sporophytes showing the deep green colour of developing setae and the gradual change to hyaline (photo by A. McLennan).

On 30 October of 2022 a small section of thallus with a well-developed calyptra was brought indoors and stored in a closed jar near a window to observe development (Fig. 7C, D). Only distilled water was provided to keep it from desiccating.

Field images were taken with a Canon G12 camera. Some images were taken by Andy McLennan with an Olympus TG-6 camera which depict more vivid colours. Micrographs were taken with a Canon 1000D camera on an unbranded compound microscope from China, with subjects mounted in water. The spore image was stacked using Hugin software. Limited sampling was done because of scarce available material.

2021 Results and Discussion

Sporophyte and its development

The 25 mm long seta of a sporophyte emerging from the calyptra took four days to reach 58 mm in length before dehiscence of the capsule. The age of the sporophyte when collected was not known.

The single capsule measured was short-ellipsoidal, 2.6 mm wide and 2.8 mm long. This is considerably larger than the capsule of *Treubia lacunosa* described by Schuster and Scott (1969) at 2 mm wide and 2.4–2.5 mm long. It consisted of four valves which folded back to release spores and elaters. The elaters

Fig. 2. *Treubia tasmanica*. A. Green seta with mature capsule. B. Dehisced capsule with elaters (photo by A. McLennan). C. Seta trans-section showing hollow centre with broken cells in the inner perimeter. D. Hyaline detached seta near calyptra (photo by A. McLennan).

are bi-spiral and long, around 850 × 9 µm (Fig. 3B), falling within the dimensions of *T. lacunosa* elaters given by Schuster and Scott (1969) as 500–1000 µm long and 5–8 µm wide. The spores (Fig. 3A) are around 28 µm in diameter and appear to contain chloroplasts.

The capsule wall of *Treubia lacunosa* was described as normally 3-stratose (occasionally with 2–4 layers), around 80–85 µm thick, although sometimes up to 95–105 µm. Cells of the middle layer are 17–24(–26) µm radially and 16–18(–24) µm tangentially. Cells of the innermost layer are considerably smaller than cells of the outer epidermal layer which have the 'capsule-wall layer of strongly bulging, convex cells' (Fig. 4D; Schuster and Scott, 1969).

The *Treubia tasmanica* capsule wall was so distinct from that of *T. lacunosa* that examination of a transverse section would suffice as a key distinguishing factor. In contrast to *T. lacunosa*, the capsule of *T. tasmanica* has valves of 6–8 cell strata with walls that are colourless and *c.* 155 µm thick (Fig. 4C). There is no obvious bulging of outer cells, but they did have a thicker epidermal layer. In transverse section, the outer cells ranged from 25–67 µm wide tangentially, and 28–40 µm deep radially. Mid-layer cells ranged from 50–72 µm tangentially and 14–26 µm radially. It was impossible to determine size of inner cells because they appeared squashed and deformed, possibly from the pressure exerted by developing spores, but cells close to the inner wall measured up to 87 µm tangentially. In capsule wall cells of *T. lacunosa*, the radial dimension is generally greater than that of the tangential, but it is the reverse in *T. tasmanica*.

The elaters of *Treubia tasmanica* did not all scatter from the capsule upon dehiscence; some persisted at the tip of the seta (Fig. 2B) which remains erect for several days. They did not appear to be attached to the capsule valves but were clustered in an unorganised manner at the tip as well as lower down on the setae. Similar clustering of elaters around dehisced capsules has been observed in *Symphyogyna hymenophyllum* (Hook.) Nees & Mont. which has connate valve tips.

The seta of *Treubia tasmanica* tapers from *c.* 1.2 to 1.1 mm in diameter and reaches 60 mm in length. In cross-section the seta consists of around 440 cells. The seta was hollow (Fig. 2C) for most of the length, but the distal few mm of the same was solid. When one decapitated seta preserved in ethanol was placed on a slide, the ethanol evaporated permitting ingress of air from both ends. A few drops of water were added to prevent dehydration and this sealed the bubbles of air. It was then possible to push a bubble from one end of the seta to the other by applying pressure progressively with the handle of a scalpel.

Duckett and Pressel (2017: Fig. 2e) show a central 'fluid-filled lysigenous cavity' in the seta of *Treubia lacunosa*. The same was observed in *T. tasmanica* (Fig. 3D). Epidermal cells of the setae are considerably smaller than the inner cells which measure around 70µm. The setae remained erect for four days or more following capsule dehiscence before desiccating. Striations on the dehisced setae on the left and right margins (Fig. 1) are cross-walls, not surface ornamentation.

The seta of *Treubia tasmanica*, on emergence from the calyptra, is a rich green, fading slightly as it lengthens (Fig. 2A at full extension and Fig. 5A), remains green-tinged for several days after dehiscence of the capsule before becoming hyaline (Fig. 2D). Setae at different stages of maturity are visible in Fig. 1.

A peculiarity of the *Treubia tasmanica* setae is that unlike those of other liverworts, e.g. Lepidoziaceae, they do not collapse in their entirety and shrink after capsule dehiscence, but dry out slowly from the distal region while the basal part remains turgid. One possible explanation for this difference is that liquid stops flowing across the transfer cells in Lepidoziaceae once setae attain maximum height but not in *T. tasmanica*.

The discovery of living plants of *T. tasmanica* with emerging sporophytes allowed their growth to be monitored over several days. *Treubia tasmanica* is not unique in having green chloroplast containing setae, but the prevalence and significance of this seems to have been largely overlooked in recent years. Availability of fresh material enables the capsule cell walls to be characterised (Fig. 4). The only on-line image of a living *T. lacunosa* sporophyte taken from a New Zealand specimen (Fig. 5C) shows the seta to be a shade of green, not hyaline. Similarly, an image of the same in a developing sporophyte is green in Glime (2021: Fig. 111). It had been assumed, but not established, that the young green seta would turn hyaline upon elongation. Hassel de Menendez (1994) says of *T. scapanioides* R.M.Schust. that the seta had 'hyaline thickened outer walls, inner cells hyaline but thin-walled' but makes no mention of cell contents, but as her study was of dried herbarium specimens, she made no mention of cell contents. Schuster and Konstantinova (1995) write of *Apotreubia hortonae* R.M.Schust. & Konstant. ex Konstant.: 'Seta 510–550 µm in diam., chlorophyllose to time of maturation of spores.' This presumably refers to the state where the sporophyte is ready to emerge from the calyptra, but there is no mention of what happens subsequently.

A recent paper by Patino *et al.* (2022: Fig. 3C) depicts mature sporophytes of *Monoclea forsteri* Hook. with indisputably green setae up to the time of dehiscence. Likewise, Pant *et al.* (2023: Fig. 1E–G) describe the newly rediscovered *Sewardiella tuberifera* Kash. from India as 'seta dull green' and depict green setae. There may be other liverworts elsewhere in the world that exhibit similar characteristics to *Treubia tasmanica* that are also worthy of further observation in the field.

Schuster (1984) noted a 'capsule with massive, chlorophyllose seta' for *Haplomitrium* and that *Symphyogyna, Pallavicinia* and *Hymenophytum* (all Pallaviciniaceae) also shared this feature. That both early diverging clades share this characteristic suggests that chlorophyllose setae could be the ancestral form from which the modern, short-lived, hyaline setae evolved.

Size of setae has no bearing on their chlorophyllose nature. *Chandonathus squarrosus* (Menzies ex Hook.) Mitt. and *Adelanthus falcatus* (Hook.) Mitt., among others, are described as having 'massive' setae with no mention of them being chlorophyllose (Engel and Glenny 2008).

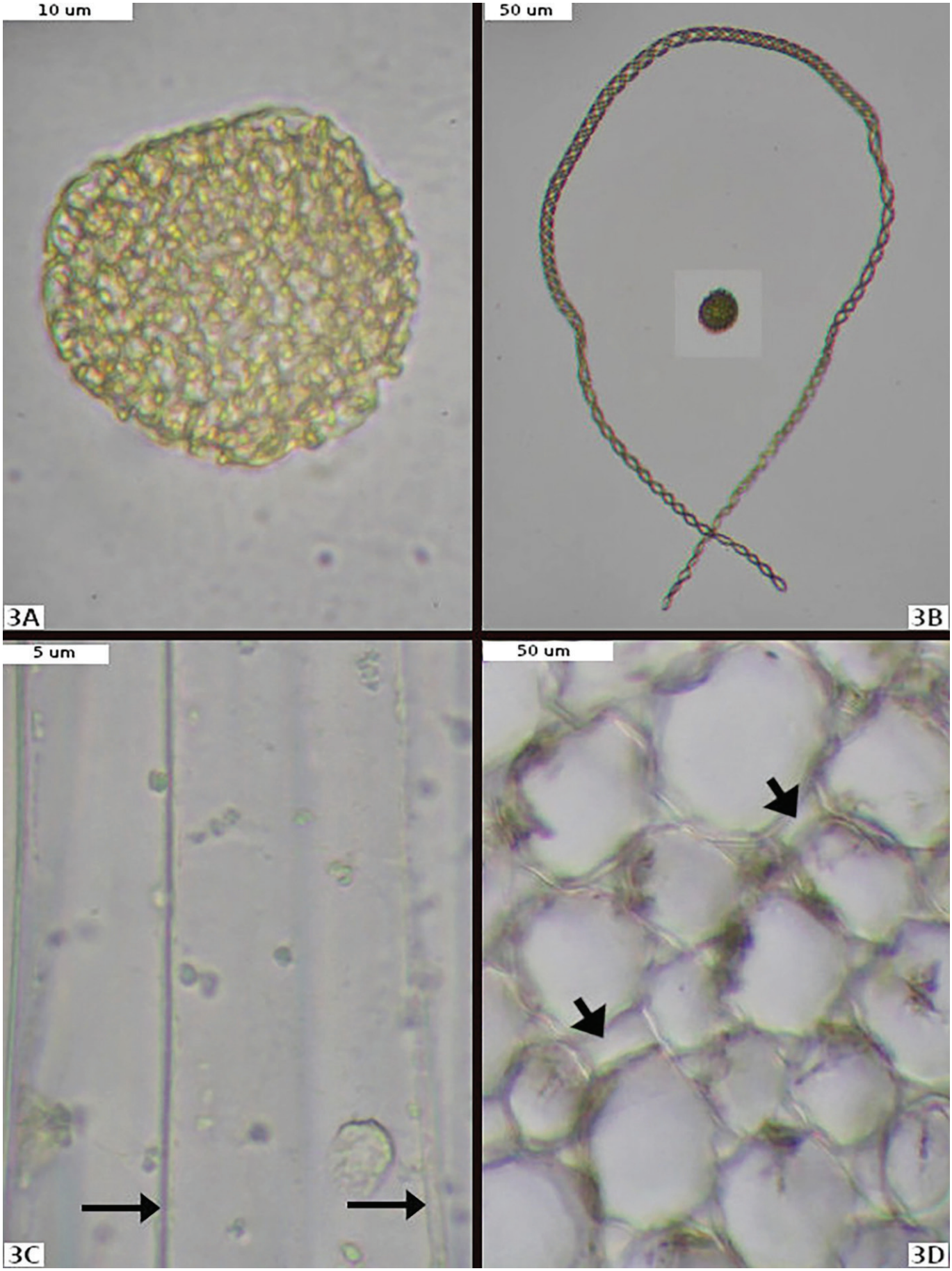

Fig. 3. *Treubia tasmanica*. A. Spore. B. Bi-spiral elater with inserted spore at same scale. C. Cell contents, walls arrowed. D. Schizogenous intercellular spaces (ICS) arrowed.

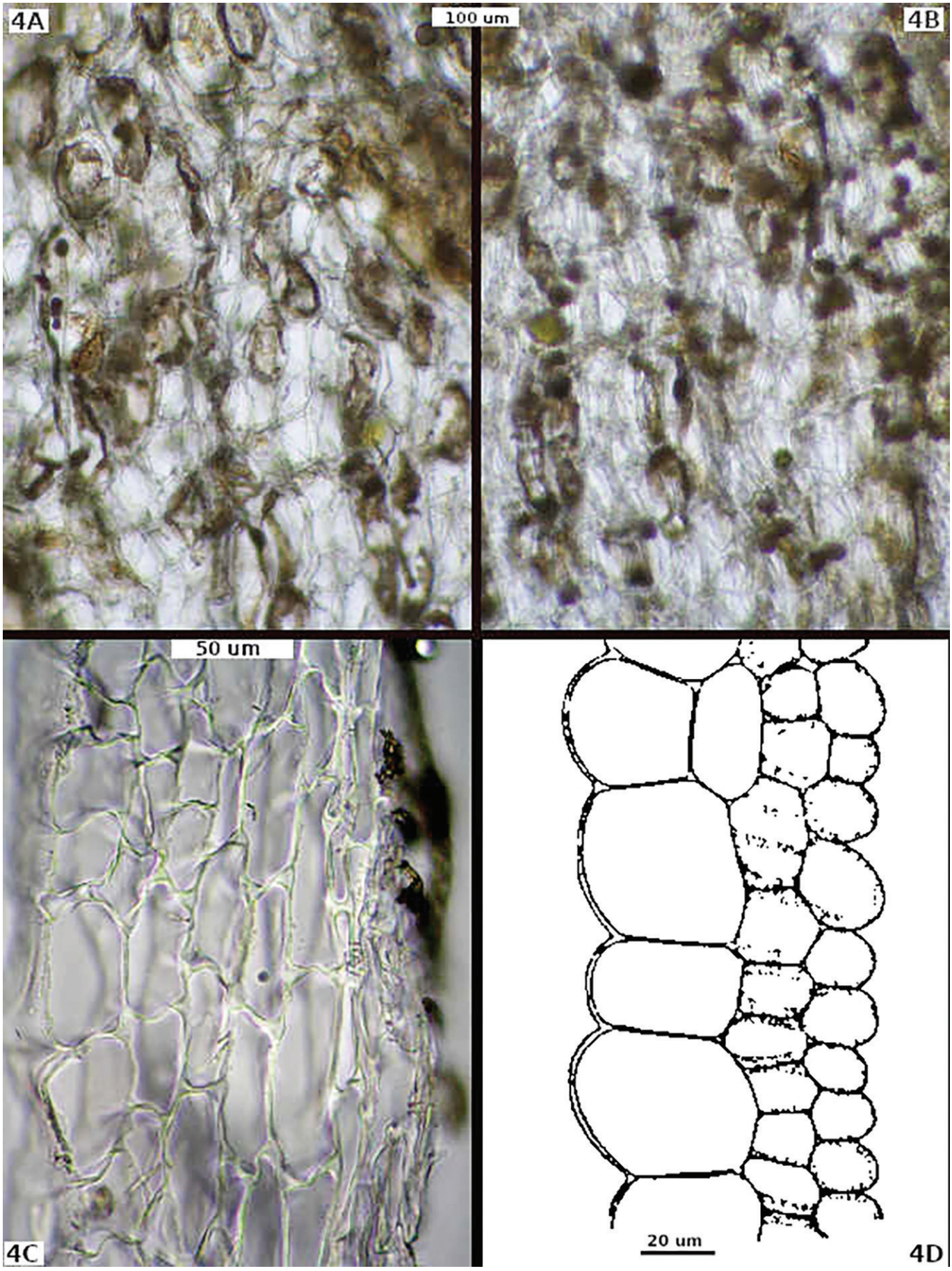

Fig. 4. *Treubia tasmanica* (A–C) and *T. lacunosa* (D). *T. tasmanica*: A. Capsule external wall. B. Capsule inner wall. C. Capsule wall transverse section. *T. lacunosa*: D. Capsule wall transverse section, republished from Schuster and Scott (1969) with permission from Hattori Botanical Laboratory.

Fig. 5. A. Young sporophyte of *Treubia tasmanica* (photo by A. McLennan). B. Sporophyte of *Goebelobryum unguiculatum* (photo by Phil Collier). C. Sporophyte of *T. lacunosa* (photo by S. Kerr from http://www.kaimaibush.co.nz/index.html). D. Dehisced sporophyte of *Pallavicinia rubristipa* (photo by A. McLennan).

If the seta's only function is to elevate the sporangia for spore dispersal, there needs to be some explanation why some persist erect for several days after capsule dehiscence. *Pallavicinia rubristipa* Schiffn. has been observed to have sporophytes taking several days to attain full extension after they emerge from the calyptra, then remaining erect for several days after dehiscing. High humidity may be ruled out as a factor since conditions under which they were stored under cover were considerably dryer than would normally prevail in their habitat in shaded rain forest. Plants of *Treubia tasmanica* described here were growing amongst Lepidoziaceae species which all had setae that mostly collapsed by early afternoon.

While it is not invariably the case that persistent setae are always chlorophyllose, it is yet to be determined if green setae always persist beyond a few hours of emerging from the perianth or shoot calyptra. *Goebelobryum unguiculatum* (Hook.f. & Taylor) Grolle had hyaline seta that persisted over several days, and possibly over two weeks (Fig. 5B) before collapsing. Initial observations indicated that it opened and closed two slits in the capsule, presumably to disperse spores when conditions were propitious. Sporophytes collected at the end of the fruiting season in early June were reported to have hardly any spores left in the capsule.

A *Chiloscyphus* sp. observed fruiting in mid-Autumn 2023 had sporophytes that took varying lengths of time to attain full setae height after capsules first fully emerged from the perianth. One isolated sporophyte that was probably several days old when first recorded took seven days to attain full height and achieve dehiscence, and it remained upright for at least another three days before collapsing.

The mechanism for fluid movement in seta cells as they elongate relies upon the schizogenous intercellular spaces (ICSs) found in 'taxa with large fleshy setae …' (Duckett and Pressel (2017: Fig. 2g) (see Fig. 3D). Duckett and Pressel (2017) go on to state that 'In liverwort setae ICSs are most likely a key structural component maintaining and augmenting the hydrostatic skeleton solely determined by the turgidity of its constituent thin-walled cells'. They state further: 'the elongated setae in several genera including members of the Haplomitriopsida (*Treubia*), Marchantiopsida (*Monoclea*), Fossombroniales (*Allisonia*) and Jungermanniales (*Wettsteinia*) contain central fluid-filled lysigenous cavities with the remains of broken cells around their periphery' (Fig. 2C). These central cavities may also play a part in the translocation of fluid and solutes within the setae.

While there are open channels for translocation of fluid within the seta there are no such pathways across the placental walls. This is effected through transfer cells, which are not only prevalent across the plant kingdom, but extend to algae and fungi as well. There is a considerable body of literature on the origins and function of transfer cells found on one or both sides of the placental wall in nourishing the sporophyte (Ligrone and Gambardella 1988; Offler *et al.* 2002; Carafa *et al.* 2003). Ligrone and Gambardella (1988) speculate that 'The persistence of sporophyte transfer cells may account for the sporophyte ability to uptake the water necessary for the elongation of the seta after spore maturation'. The prevailing view expressed recently is that 'In this intergenerational zone, specialized cells facilitate an intensified flow of solutes to the sporophyte that is dependent on the persistent gametophyte' (Henry and Renzaglia 2021). Transfer cells consist of membranes, not unidirectional valves, so there is no reason why the flow could not reverse.

2022–3 Observations and Discussion

The same population of *Treubia tasmanica* observed above came into fruit again the following two seasons and provided an opportunity to record sporophyte development over an extended period. Calyptra appeared as well-developed, prominent, spherical protuberances on thalli (Fig. 6A) when first observed on 21 September 2022. Judging from photographs, there was no perceptible increase in diameter over a period of nine weeks until capsules emerged, but as no observations were made of calyptra height, growth might have occurred over that time without being noticed. There was considerable size difference between the largest calyptra and the smallest, but this was not due to maturity as the capsule from a smaller calyptra emerged two days earlier than that of the larger. The capsule on the right in Fig. 6C was about 30% wider than that on the left.

No measurements were taken in the field in 2022 but a few calyptra were observed in the same population in mid-May of 2023 and one was measured having a diameter of *c.* 1.2 mm. This grew to 1.8 mm five weeks later. There was a mishap with the main sporophyte that was being monitored (emergent capsule in Fig. 6B). Rain over several days caused the tip to droop over until the capsule touched the ground. Nevertheless, the seta remained partially green at the base and did not shrivel to the base until 24 November 2022.

A summary of development based upon the exposed capsule in Fig. 6B follows:

- the entire capsule had emerged from calyptra on October 31, but the seta was not visible;
- it took six days for the seta to attain maximum height (Fig. 6C), on November 6, before the capsule began dehiscing the following day (Fig. 6D);
- the seta remained upright for another seven days, until November 14, when it started drooping;
- the green seta with dehisced capsule slowly faded to hyaline over another ten days (Fig. 7B, arrowed), before it shrivelled to the base on November 24, giving it a life of 23 days.

Schuster's (1984) explanation of the capsule dehiscing mechanism was that upon exposure to the atmosphere the outer cells dry out and the valves shrink transversely thus setting up forces that rupture the vertical sutures. The developing sporophyte of *Treubia tasmanica* collected the first season was stored under conditions much drier than found in its natural habitat yet failed to dehisce until the seta was fully extended four days later. In the second season it took seven days for the emergent capsule to dehisce (Figs. 6B, 6C and 6D). Weather conditions were near perfect with warm sunny days. Other bryophytes in the vicinity, mainly Lepidoziaceae and *Chiloscyphus* sp., had sporophytes dehiscing by mid-day every day during this period.

Fig. 6. *Treubia tasmanica*. A. First observation of enlarged calyptra on 21 September 2022. B. Capsule emerged from calyptra on 31 October 2022. C. Seta attained maximum height on 6 November 2022. D. Capsule dehisced on 7 November 2022.

Fig. 7. *Treubia tasmanica*, 2022. A. Capsule valves closed to protect elaters and spores in damp weather, 12 November (insert is a different sporophyte observed on 18 November). B. Arrowed seta faded to hyaline before shrivelling on 23 November. C. Capsule emerging from calyptra grown indoors on 31 October. D. Sporophyte grown indoors. i) 2 November; ii) 5 November (seta attains maximum height of 34 mm); iii) top: Capsule dehisced on 6 November; bottom: Capsule valves closed on 7 November.

However, drying of the capsule wall in *Treubia tasmanica* could not be excluded as one of the factors influencing dehiscing. The sporophyte kept indoors was taken out of the closed container and exposed to the atmosphere six days after the capsule had emerged (Fig. 7Dii). It promptly dehisced quarter of an hour later, after which it was returned to the humidity of the closed jar. A peculiarity of *Treubia tasmanica* is its ability to close the capsule valves under moist conditions. Figure 7Diii shows the start of dehiscing (top) but a day later the valves had closed (bottom).

The situation in the field was no less remarkable. It had rained overnight and part of the morning on November 12. The fuzzy setae apex that was present the previous day had disappeared and in their place were entire capsules, a little deformed but nevertheless fully enclosing residual elaters and spores (Fig. 7A). The shiny appearance suggests water had filled the capsules and was encapsulated. It is possibly the weight of this water that caused the tall sporophyte to droop. Photo insert shows a different sporophyte from November 18 which shows no such shininess. They remained this way for four days, but the anticipated reopening of capsules was not observed. When the weather turned dry, the capsule valves had shrivelled, exposing some elaters, but not in the quantities present earlier.

The sporophyte taken indoors was phototrophic. It was possible to change the inclination by twisting the jar to face different directions.

The change in seta colour as it lengthens is particularly interesting. Garjeanne (1932) cites an experiment by Du Buy and Nurnbergk (1932) on *Pellia epiphylla* (L.) Corda which showed that seta growth took place mainly at the proximal end. If this were the case for *T. tasmanica* there ought to be a colour gradient from the base to the tip, but this is not so. Setae lengthen not by cell division but by cell elongation. In Figs. 6C, 6D and 7D the colour lightens as the seta lengthens suggesting the cells were expanding uniformly and the chloroplasts were diffusing into larger volumes.

It is at least a plausible hypothesis that the seta nourishes the sporangia during the brief period between emergence and dehiscing. It is not implausible that the spores grow in size during this period, which could explain the internal pressure needed to stress the capsule walls to the point they would burst open under dry conditions. The presence of apparently compressed cells in the inner capsule wall (Fig. 4C) would support this supposition.

Why the green seta remains attached to the gametophyte after the sporangia dehisces, and slowly fades to hyaline over a fortnight, is a thorny problem. In the absence of competing alternatives one possibility is that they are going into senescence where the chloroplasts transform into solutes which flow back into the gametophyte.

Our current understanding holds that young setae of at least some species of liverworts in compressed form are green. Schuster (1984) made passing reference to this: 'Prior to elongation, cells may seem strikingly chlorophyllose ...' but does not amplify on the subject. Puri (2011) stated that 'The cells of the immature foot and seta, the wall of the capsule and the elaters (of *Marchantia polymorpha* L.) contain chloroplast ...'. It is reasonable to question if the function of these chloroplasts is to provide nutrition to the developing sporophytes or if they are merely remnants of once functional organelles that have outlived their purpose. If the first case holds, several questions then arise (D.C. Cargill, pers. comm.): What is the process that nourishes the sporophyte after it emerges from the calyptra/perianth? Is it provided solely by the seta, or does it also receive nourishment from the gametophyte? Does the flow of nutrients stop upon the capsule dehiscing or is there a reverse flow into the parent?.

While the contribution of the seta to nourishing the gametophyte, if established, may be small it is not negligible. Some of the *Treubia* sporophytes were emerging from thalli that were hidden by overgrowth of other more vigorous bryophytes and grasses so even a brief period of photosynthesis may help keep the plants alive for another season.

Since *Treubia tasmanica* setae do not wilt for around two weeks after they are fully extended, it follows that the gametophyte has to continue pumping water across the transfer cells to keep the setae turgid. The hollow liquid filled central cavity of the seta, which extends almost to the top, simplifies matters. Fig. 7Dii shows water droplets adhering to the seta kept in a jar. On the assumption that condensation was more likely to have formed on the glass jar subject to temperature fluctuations, this is probably water from guttation. However, this has to remain conjecture for the present.

Renzaglia *et al.* (2007) summarised some widely held dogmas thus: 'Liverwort sporophytes remain enclosed within gametophytic tissue until the spores are mature. Sporangia are then elevated solely by rapid elongation of seta cells acting as a hydrostatic skeleton. The seta is ephemeral, lacks internal differentiation and is completely intolerant to desiccation.'

Treubia tasmanica appears to provide an exception to the rule. The claim that spores mature within the gametophyte is at least questionable. It has been reported that '*Fossombronia* capsules that have been elevated upon elongated setae may still have immature spores' (D.C. Cargill, pers. comm.). These spores were extracted from emerged capsules that had yet to dehisce. The seta is (relatively) slow growing, chlorophyllose and (semi)persistent. Puri (2011) wrote that 'In some sporogonia of *P(ellia) epiphylla*, the seta increases in length from 1 millimeter to as much as 80 millimeters in three to four days.' It is surprising that this extended life of sporophytes is not more widely known, since the book was first published in 1980. There are reasonable grounds for believing that the seta plays a part in nourishing the sporangia during the final days of maturity.

This paper is a first attempt to try and explain unusual phenomena and it is possible that wrong inferences may have been drawn. They are presented as the best interpretations available in the face of incomplete knowledge. Apart from the species discussed here, as well as *P. epiphylla*, it remains to be seen if other taxa with chlorophyllose setae mentioned by Schuster (1984), the Treubiales and *Monoclea forsteri* likewise have semi-persistent setae which remain erect after capsules dehisce and spores disperse. Morphological characteristics not previously published for *Treubia tasmanica* are presented below.

Taxonomy

Treubia tasmanica R.M.Schust. & G.A.M.Scott, *J. Hattori Bot. Lab.* 32: 248, figs 1(1–5), 2(5), 4(2), 5(1–5) (1969). *Type*: Tasmania: near Camp Creek, along Lyell Highway, west of Derwent Bridge, Surprise Valley, on slopes of Mt Arrowsmith, *R.M.Schuster 50376* (Holotype: F C0172296F).

Treubia insignis Goebel *sensu* Rodway, *Pap. Proc. R. Soc. Tasmania* 20 (1916).

Discovery of a second fruiting population in 2023 (CANB 999918) permitted study of the gametophyte, which had not previously been observed for *Treubia tasmanica*. This was growing on a sloping rock surface covered with organic debris. Accompanying bryophytes were *Lepidozia procera* Mitt., *Gackstroemia weindorferi* (Herzog) Grolle, *Wijkia extenuata* (Brid.) H.A.Crum and a *Bazzania* sp.

Basal parts of many plants were e-chlorophyllose but were still alive judging from mucilage below the axis. They were mostly under 25 mm in length. Vigorous plants measured up to 10.5 mm across the leaves, a little wider than Schuster and Scott's (1969) description of 5–9 mm wide. Branching was sparse, but there were up to three lateral branches on the main shoots. In general, there appeared to be little contact between the ventral axes and the substrate, other than through the intermediary of mucilage. Some rhizoids were branched. Although most fruiting plants sported only a single sporophyte, a few had two.

When describing *Treubia tasmanica*, Schuster and Scott (1969) mentioned 'mucilage plentiful, colourless'. *Treubia* mucilage was studied in detail by Duckett *et al*. (2006) who examined live thalli of three New Zealand species (subsequently reduced to two – *T. lacunosa* and *T. pygmaea* – in Glenny *et al*. 2015). They reported that thalli not only produced copious amounts of mucilage, but were also capable of replenishing it if this was removed and the thalli was placed in water. The same was observed for *T. tasmanica* where plants collected after rain had a thick layer of mucilage, especially on newer growth, but mucilage was present along the whole ventral axes. This shrank when stored in a humid container, but grew again when immersed in water for several hours (Fig 9D).

Oil bodies were present in most but not all lateral leaf cells which tended to decrease in size from leaf median to border (Fig 8A). Most of the leaf cells contained solitary oil bodies (Fig. 8B) but a few had up to four. Examination of lateral leaves less than four hours after collection displayed oil bodies that had largely lost their integrity and appeared as amorphous blobs (Fig 8C). An explanation of this could be found in Schuster (1992) who stated that 'the high light intensity (and heat) transmitted and concentrated through the Abbe condenser of the light microscope results in rapid disintegration of the bounding membrane and release of the lipid droplets'. Dried specimens that had been re-hydrated showed lipid droplets occupying almost the entire cell lumen. The few cells devoid of oil bodies were densely packed with cylindrical chloroplasts (Fig 8D). The green background is the effect of superimposition over multistratose cells below.

Schuster and Scott (1969) state 'Scattered axial cells with oil-bodies 135–170 µm long × 45–80 µm wide, more or less filling the cells in which they occur' without specifying which part of the axis they were referring to. This averages out to 153 µm × 63 µm giving a ratio of 1:2.4, somewhat higher than the oil body of the lateral leaf (Fig 8B) which measures 32 × 21 µm with a ratio of 1:1.5. Oil bodies retaining integrity in the specimen examined do not fill the cell lumen but may provide that illusion when lipids spill from the membrane (Fig 8C). Oil bodies from the calyptra vary greatly. Those from the distal part surrounding the capsule are somewhat regular in shape (Fig. 8E) while those surrounding the setae are greatly elongated, to over 1:5.5 ratio (Fig 8F). Since these cells would have originated from a pre-elongated state, it may be assumed that the oil bodies were once more regular and elongated as the cells stretched in one direction.

Although the calyptra appears green, and there are a few chloroplasts in the cells, it is mostly clear. It is the young seta which provides the appearance of green colour. It is about 10 mm high and 2.9 mm wide. Radially it consists of 10–12 cells and is approximately 0.21 mm thick (Fig. 9B). This is comparable to Schuster and Scott's (1969) description of *T. lacunosa* with 'lower third of calyptra *ca*. 8–12 cells thick'. Although the sector depicted here shows no oil bodies, they were present, mainly in the outer layer of cells, but a few were observed in inner cells as well.

There is an apparent discrepancy in that the thickness of calyptra walls together with that of seta (admittedly measured on different plants) do not add up to calyptra width. A similar discrepancy may be found in *T. lacunosa* where the calyptra width averages about 3 mm and the seta is 0.7 mm thick (Glenny *et al*. 2015), which makes each wall 1.15 mm wide. This is considerably thicker than that of *T. tasmanica* with walls of 0.21 mm thickness. A possible explanation for this discrepancy in both cases could be that the compressed seta within the calyptra has greater girth than that of the emerged seta.

Specimens examined relevant to discussion

Treubia tasmanica: Poimena, Blue Tier, 100 m along Moon Valley Rim Circuit, 13 Nov. 2021, 41°11'54.24"S, 148°00'19.92"E, 761 m, *T. Thekathyil 301* (HO 615113); Poimena, Blue Tier, 2.9 km along bike trail to Weldborough, 23 October 2023, 41°11'28.38"S, 148°00'59.46"E 750 m, *T.Thekathyil 312A* (CANB 999918).

Pallavicinia rubristipa: Three Notches Track, Blue Tier, 30 m north of first bridge, 29 Nov. 2021, 41°11'13.62"S, 148°00'35.34"E, 722 m, *T. Thekathyil 302* (HO 615114).

Goebelobryum unguiculatum: Port Sorrell, 100 m NE of nearby house, 04 June 2014, 41°11'08.70"S, 146°32'42.06"E, 9 m, *T. Thekathyil 168* (HO 578885, CANB, CAS, F).

Chiloscyphus sp., Lottah, 100m east from end of Gould St. 20 Apr. 2023, 41°13'13.02"S, 148°01'27.24"E, 325 m, *T. Thekathyil 303* (HO 615115, CANB, CAS).

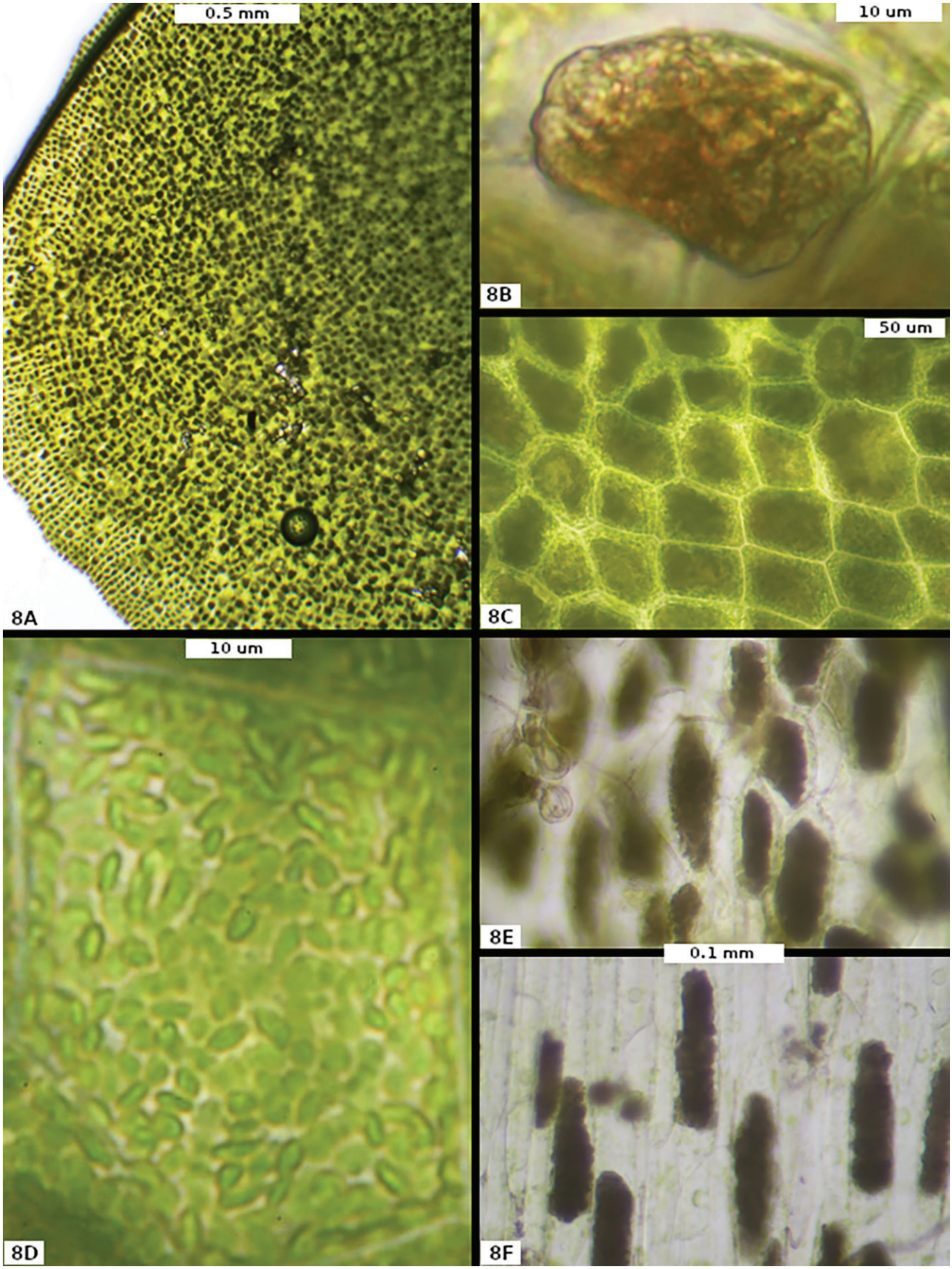

Fig. 8. *Treubia tasmanica* (CANB 999918 population). A. lateral leaf showing cell size decreasing towards border. B. Intact oil body. C. Oil bodies releasing lipid droplets into cell lumen. D. Chloroplasts in cell devoid of oil bodies. E. Oil bodies from upper region of calyptra covering capsule. F. Oil bodies stretched to fit elongating calyptra cells from lower region.

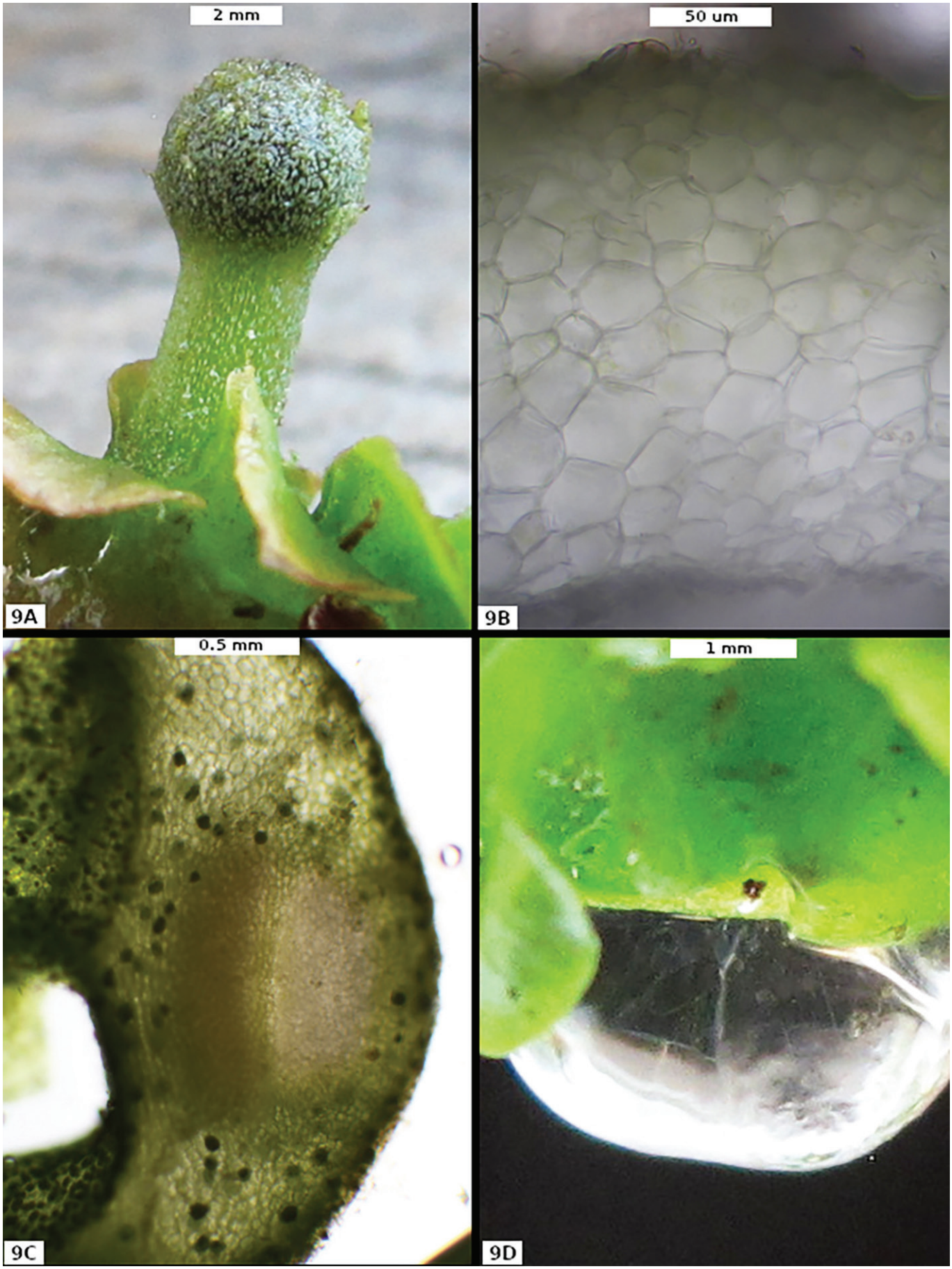

Fig. 9. *Treubia tasmanica* (CANB 999918 population): A. sporophyte ready to emerge from calyptra. B. Transverse section of calyptra wall. C. Transverse section of shoot axis showing scattered oil bodies. D. Mucilage below shoot axis after soaking in water.

Acknowledgements

I am grateful to the following parties for their help: Rod Seppelt initially suggested writing up notes for publication and has provided invaluable editorial guidance in preparing the manuscript. He and Chris Cargill read through multiple versions of the manuscript and made valuable suggestions on improving it. Neither party is responsible for any wayward ideas espoused here. Andy McLennan of Lottah provided photos for Figures 1, 2B, 2D, 5A and 5D. Phil Collier provided the photo of *Goebelobryum unguiculatum* (5B) as well as granted permission to collect specimens from his property at Port Sorrell. Shirley Kerr of New Zealand permitted use of the *Treubia lacunosa* sporophyte image on her website http://www.kaimaibush.co.nz. Hattori Botanical Laboratory granted permission to reuse the drawing of *T. lacunosa* capsule wall (Fig. 4D) from *Journal of the Hattori Botanical Laboratory* 32: 262. I am grateful to the anonymous referee who made some very pertinent comments on the paper which I have tried to address. Tasmanian Department of Primary Industries, Parks, Water and Environment granted the collection permit for specimens.

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