Early land plants from the Lower Devonian of central Victoria, Australia, including a new species of *Salopella*

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Abstract

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Early land plants with elongate sporangia held in the palaeobotanical archives of Museums Victoria were examined. The fossil plants are from Yea (?upper Silurian) and near Matlock (Lower Devonian) in central Victoria, and are of interest because they contribute to our understanding of the evolution of early land plants in a region in which research has been limited. Both *Salopella australis* and *Salopella caespitosa* were originally described over 30 years ago and this reinvestigation has resulted in the emending of the diagnosis of *Salopella australis* and the erection of a new morphotaxon *Salopella laidae* sp. nov. based primarily on differing branching architecture and sporangial morphology. *Salopella laidae* comes from Yea Formation and possesses regular isotomous branching over at least two orders of branching, terminating in elongate sporangia that are wider than their subtending axes, differing from *S. australis,* which possesses only one dichotomy emanating from at least two erect parallel parent axes with sporangia that are the same width as their subtending axes. A recently collected specimen of *Salopella caespitosa* was also examined and adds to our understanding of this taxon, which was previously only known from one specimen. Consideration is given to the possible sources of these early land plants based on other early land plants with a similar grade of organisation.

Keywords

embryophytes, rhyniophytoids, *Baragwanathia* flora, Devonian, Victoria

Introduction

Fossil plants have been known in Victoria since the 19th century (Nicholas, 1875). Palaeobotanical studies on the *Baragwanathia* flora (Jaeger, 1966) from the Silurio-Devonian of Australia have primarily been limited to the first half of the twentieth century (Cookson 1935, 1937, 1949; Lang and Cookson, 1927, 1930, 1935) and further expanded with Tims (1980), Tims and Chambers (1984) and McSweeney et al. (2020). The majority of plant fossils have been uncovered in the Melbourne Zone (fig. 1), and some further fragmentary remains have been found further south in the Mathinnia Group of northeastern Tasmania (Baillie et al., 1989; Banks, 1962; Cookson, 1937; Powell et al., 1993). New data on early land plants from Australia, which was once part of northeastern Gondwana during the Silurio–Devonian periods, is of significance globally because it allows comparisons between floral assemblages in Laurussia (Europe, the United States and Canada), mid-palaeolatitude (Argentina) and high palaeolatitude (Bolivia and Brazil) western Gondwana sites and Chinese sites (North and South China Plates; Torsvik and Cocks, 2019). Furthermore, the new data allow for more

data to be acrued to test the hypothesis of a Lower Devonian northeastern Gondwana phytogeographic unit within which both South China and Australia were parts or subunits of, according to Hao and Gensel (1995, 1998, 2001) and Wang et al. (2002).

This paper records one new taxon after an investigation of early land plant material with elongate sporangia collected by Tims and Chambers (1984) from the ?upper Silurian–Lower Devonian Yea Formation, the Humevale Formation near Yea and the Lower Devonian Wilson Creek Shale Formation near Matlock in central Victoria (fig. 1). Early land plants possessing elongate sporangia with tapering apices of either rounded or pointed tips and with fusiform or elongate parallel sided sporangia characteristic of rhyniophytes/rhyniophytoids (*sensu* Edwards & Edwards 1986) were described by Tims and Chambers (1984) and assigned to *Salopella australis* and *Salopella caespitosa*. The specimens described herein are compressions/impressions with little anatomical detail preserved and belong to the same morphogenus *Salopella* Edwards and Richardson, 1974. One new specimen of *S. caespitosa,* only the second so far recorded, was also

examined and is of siginifcance to our understanding of this morphotaxon because it was preserved in semi-relief as a coalified compression/impression.

Locality, stratigraphy and age

The Melbourne Zone is a triangular stuctural region occuping central Victoria bounded by the Heathcote Fault in the west and Governor Fault in the east, opening towards the south (VandenBerg and Gray, 1988). The Wilson Creek Shale extends across the Melbourne Zone (VandenBerg, 1975; VandenBerg et al., 2006), and based on the conodont fauna, is considered to be middle Pragian–Emsian (Mawson and Talent, 1994). It comprises mudstone and shale units, characteristic of deep water and anoxic conditions, with *Uncinatograptus thomasi* (=*Monograptus thomasi*) Jaeger, 1966, found throughout and *Neomonograptus*

notoaequabilis (=*Monograptus aequabilis notoaequabilis*) Jaeger et al., 1969, in the upper half (Edwards et al., 1997, 1998; Lenz 2013; VandenBerg, 1988; VandenBerg et al., 2006). The outcrop examined occurs on Frenchmans Spur track, approximately 10 km west of Matlock, and is the type location of the rhyniophytoids *Salopella australis* and *S. caespitosa*, and the early "trimerophyte-grade" (*sensu lato* Banks 1975) plant *Dawsonites subarcuatus* (Tims and Chambers, 1984).

The Humevale Siltstone and Yea Formation occur in the western part of the Melbourne Zone (Edwards et al., 1997; VandenBerg, 1988) and both are exposed near Yea. The dating of the exposures at Ghin Ghin Road and Limestone Road, Yea, as Pridolian and Ludlovian respectively by Garratt and Rickards (1984, 1987), Garratt et al. (1984), Rickards and Garratt (1990), and Rickards (2000) are contentious for a number of workers (Banks 1980; Cleal and Thomas, 1999;
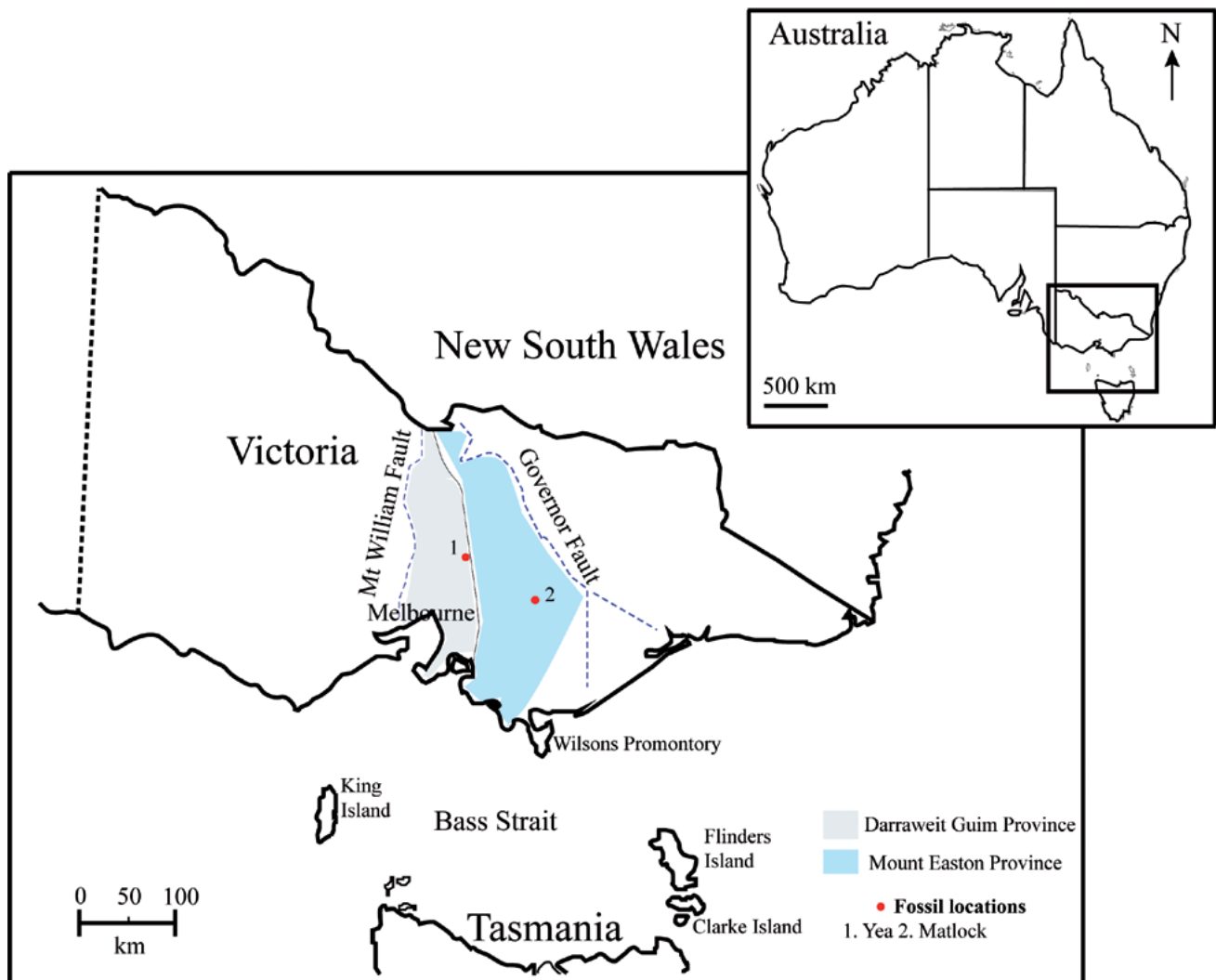

Figure 1. Map of Victoria, Australia, showing the fossil locations within the Melbourne Zone. Location 1. Yea, Ghin Ghin Road, Limestone Road (37° 12.38' S, 145° 25.39' E). Location 2. Matlock, Frenchmans Spur (37° 25.82' S, 146° 77.24' E.), the type location of *Salopella australis* and *S. caespitosa* (Tims and Chambers, 1984). Source: adapted from Moore et al. (1998: fig. 2).

Edwards et al., 1979; Edwards et al., 1997; Hao and Gensel, 2001; Hueber, 1983, 1992). Hueber (1983) considered the morphological and anatomical complexity of *Baragwanathia longifolia* more akin to a Lower to Middle Devonian age and noted the complex nature of the conspecific taxa *Yarravia (=Hedeia)* to further that point, McSweeney et al. (2021). Hueber (1992) suggested differences between the *Baragwanathia* from the two horizons at Yea were likely intraspecific and considered the interpretation of graptolites by Garratt and Rickards (1984) as subjective because preservation was poor. Additionally, Hueber (1992) highlighted that the purported 24 million year difference between the two horizons had resulted in little evolutionary change, as did Hao and Gensel (2001: 103), yet massive differences occurred over 3 million years between the *Cooksonia* spp. found in Ireland (Edwards et al., 1983) and the younger Lower Plant Horizon of Yea. Edwards et al. (1979: 321) questioned the interpretation of the age of *Maoristrophia banksi* and the graptolites not occurring on the same plane as the *Baragwanathia* in the Lower Plant Horizon. Finally, Edwards et al. (1997: 22) consider the Humevale and Yea Formations at Yea to be part of the Norton Gully Sandstone Formation.

The Yea and Humevale Formations espoused by Garratt (1978) are retained because they provide a stratigraphic framework for the area (McSweeney et al., 2020: fig. 2 – stratigraphical comparison chart and Ghin Ghin Road exposure). However, a Lower Devonian age will be used when assigning an age to specimens at Yea to account for these differing interpretations.

Materials and methods

The collection site of early land plants from Limestone Road, Yea, is heritage listed, with further collecting forbidden; in addition, the Frenchmans Spur locality is heavily overgrown and, for the most part, inaccessible. The specimens described herein are from Museum Victoria's palaeontological archives and were collected by J.D. Tims and J. Douglas in the 1970s and early 1980s, and one specimen *S. caespitosa* (NMV P235941) collected by C. Earp and M. Pepper, 19 m from the Devil's Elbow road cutting on Ghin Ghin Road, Yea, central Victoria, Australia.

The specimens collected by Tims and Douglas are preserved as fine compressions/impressions, and even after maceration with Schultze's solution and acetate film pulls (see Tims and Chambers, 1984: 266), no evidence of internal anatomy remains. The *S. caespitosa* collected by Earp and Pepper is coalified and a fragment was taken from the lowest part of the parent axis of NMV P235941.2 using a fine steel needle. Additionally, a fragment was dislodged from the centre of the basal dark presumed sporogenous region of sporangia two and four on NMV P235941.1. These fragments were placed onto aluminium stubs for scanning electron microscope analysis under low vacuum on an FEI Quanta 200 ESEM at RMIT University's RMIT Microscopy and Microanalysis Facility (RMMF).

Images were taken at Museums Victoria (Carlton) using a Leica M205 C microscope and Leica Application Suite software version 3.8.0. Images were edited using Adobe Illustrator CC 2017 and morphological measurements were taken using ImageJ software. Dégagement was undertaken on the Museums Victoria material archived by Tims (1974, 1980), Tims and Chambers (1984) and J. Douglas.

Institutional abbreviations

NMV P, Museum Victoria Palaeontology Collection, Melbourne, Australia. The use of .1 and .2 at the end of NMV P refer to part and counterpart, respectively. All specimens including the samples placed on stubs for scanning electron microscope analysis are housed in the Palaeontological Section, Museums Victoria, Melbourne.

Systematic palaeobotany

Plantae. *Incertae sedis*

Genus. *Salopella* **Edwards and Richardson, 1974**

Type Species. *Salopella allenii* Edwards and Richardson, 1974
Salopella australis Tims and Chambers, 1984 (fig. 2A–G; line-drawing fig. 6A)
Salopella australis Tims and Chambers (1984: pl. 32, figs. 1–6; pl. 34, figs. 4, 5; text-fig. 2A–C)

Emended diagnosis (after Tims and Chambers, 1984). New information in bold. Axes 0.9–2.4 mm wide with central line, **at least two long aligned parallel parent axes** with **one dichotomy each resulting in narrower shorter daughter axes terminated by a single sporangium on each.** Plant at least **80 mm high**. No obvious branching at the base of the sporangia. Sporangia 6.5–14.0 mm high and 1.3–2.0 mm wide, with parallel sides in the lower two-thirds of the presumed fertile portion. Sterile sporangia apex tapering to a point in the upper third. Spore characters unknown.

Locality. Frenchmans Spur Track, 10 km west of Matlock, Victoria. 37° 25.82' S, 146° 77.24' E.

Stratigraphy and age. Wilson Creek Shale, mid-Pragian–Emsian, Lower Devonian (Carey and Bolger, 1995; Mawson and Talent, 1994).

Note: Two specimens assigned to *S. australis* by Tims and Chambers (1984) from Limestone Road have been transferred to Gen. et sp. indet. because the specimens are too poorly preserved to unequivocally assign to any taxon. These are NMV P229617 and NMV P157323; NMV P157323 (Jack Douglas Private Collection) was figured by Tims and Chambers (1984: pl. 32, figs 5, 6 and text-fig. 2b) but possesses a completely different branching architecture to the holotype for *S. australis* and has poorly defined sporangia. Specimen NMV P157323 has been re-drawn here (fig. 6B) for comparison to *S. australis* (fig. 2A–E). Specimen NMV P50011 from Limestone Road has been moved out of *S. australis* to a new *Salopella* species (see below). Most specimens assigned to the Wilson Creek Shale by Tims and Chambers (1984) on Frenchmans Spur track are considered *S. australis* because they have subtending axes the same width

as their sporangia (e.g. NMV P50014, NMV P33219 and NMV P50008 [holotype]). Only in cases where this character is equivocal are specimens assigned to Gen. et sp. nov. (e.g. NMV P50010).

Description. *Salopella australis* possessed an erect habit with at least two long parent axes aligned parallel to each other and with one distal dichotomy on each resulting in narrower shorter daughter axes, each terminating in an elongate sporangium with an acuminate apex. A slight indentation occurs on some sporangia at the darker carbonaceous area and sterile interface, and proximally the dark carbonaceous area tapers inwards on the daughter axes.

Remarks. A reassessment of the morphospecies *Salopella australis* as originally determined by Tims and Chambers (1984) has necessitated the removal of some of the specimens attributable to it, primarily due to differing branching architectures and poor preservation. Tims and Chambers (1984: 268) noted four species with two dichotomies, but only three were found; presumably, the fourth is in a private collection. Nonetheless, all the specimens figured in Tims and Chambers (1984) were examined. Tims and Chambers (1984: 270) described *S. australis* as "open-branched" (Tims and Chambers, 1984: pl. 32, fig. 5, 6) with at least two dichotomies of widely dichotomising daughter axes emanating from one parent axis, and up to at least 145 mm in length (fig. 6B). However, this was found to occur on only three specimens from Limestone Road and was not found on the holotype (fig. 2D, E – double arrows between aligned parent axes).

The holotype possessed two aligned parent axes, with one of the parent axes dichotomising into shorter narrower daughter axes. The other parent axis was not as well preserved. However, another specimen with better preservation (fig. 2A, C) shows both parent axes aligned and dichotomising into shorter narrower daughter axes terminated with elongate sporangia that are no wider than their subtending axes. Tims and Chambers (1984: pl. 32, fig. 4) partly illustrated this specimen with only one of the parent axes shown. However, Tims and Chambers (1984) did not mention or show the other parent axis aligned parallel to this axis. Furthermore, there was an additional specimen in the collection not figured by Tims and Chambers (1984), likely due to its poor preservation, but which also had two aligned almost parallel axes and is similar to the holotype with two parent axes aligned and with one of the parent axes possessing a single dichotomy with short daughter axes terminated in elongate sporangia (fig. 2B). Even taking into account the effects of degradation of the specimens before fossilisation and the effects of ocean currents on orientation of the axes, the Limestone Road specimens appears to have more in common with *S. caespitosa* than *S. australis*, with two dichotomies and relatively longer daughter axes from the ultimate dichotomy (fig. 6B).

This emendation has resulted in the maximum known length of *S. australis* being reduced from 145 mm to 80 mm and the reduction of known dichotomies to one, with the sporangial dimensions and morphology remaining the same. Specimens attributed to *S. australis* herein (fig. 2A–E) were

deposited in a deep marine quiescent environment of the Wilson Creek Shale, and like the holotype, possessed parallel erect axes. This branching architecture of erect parallel aligned axes was found only in three specimens, including the holotype. All the other specimens bar one, which is defined below, are too poorly preserved to attribute to any taxon. Parsimony suggests that parallel axes that dichotomise at the same level, with axes of comparable widths, terminating in elongate sporangia on short daughter axes also of equal dimensions, that have been transported a considerable distance belong to the same plant (*sensu lato* Wang and Hao, 2004; Edwards et al., 2015; Edwards and Li, 2018a) and are representative of its true branching architecture. We acknowledge that we have failed to show organic connection, and current alignment could conceivably result in this axial configuration, but the likelihood of this occurring to three separate specimens with characters such as branching and sporangia occurring at the same height and with the same dimensions is unlikely. We postulate that the parallel aligned axes may have emanated from a rhizomatous region because there was no converging of the parent axes. Two of these parallel aligned specimens were included in Tims and Chambers (1984) but noticeably in both cases, only one of the parent axes was visible (Tims and Chamber, 1984: text-fig. 2A, pl.32, figs. 1, 2, 4). Additionally, the line-drawing of *S. australis* in Tims and Chambers (1984: text-fig. 2a) shows the daughter axes of the parent axes with slightly differing lengths, which was based on Tims and Chambers (1984: pl. 32, fig. 1). But a closer examination of this specimen (holotype; fig. 2D) shows the daughter axes are preserved on different levels of lamina, with the perceived shorter daughter axis (upper arrow) partly obscured by another axis.

The specimens removed from *Salopella australis* (Tims and Chambers, 1984: pl. 32, figs 3, 5) and placed in Gen. et sp. indet. include isolated poorly preserved sporangia from both the Wilson Creek Shale on Frenchmans Spur (fig. 2F, G) and specimens from Limestone Road because the preservations were generally poor and the branching architectures greatly differed to the holotype. One of the excluded specimens (Tims and Chambers, 1984: pl. 32, fig. 3) with differing branching architecture to *S. australis* is described below as a new morphospecies. Thus, *S. australis* is no longer represented in the flora of the Lower Plant Horizon.

Salopella caespitosa Tims and Chambers, 1984 (fig 3A–I (holotype) and fig. 4A–E)

Material: NMV P50016 (holotype) and NMV P235941 both with part and counterpart.

The circumscription of *Salopella caespitosa* was based on a single specimen with its counterpart from the Wilson Creek Shale Formation on Frenchmans Spur Track approximately 10 km west of Matlock in central Victoria. No new data have been added on this taxon since its inception. The discovery of a new specimen from the base of the Humevale Formation on Ghin Ghin Road near Yea preserved in semi-relief contributes information on its dimensions, gross morphology and temporal range.
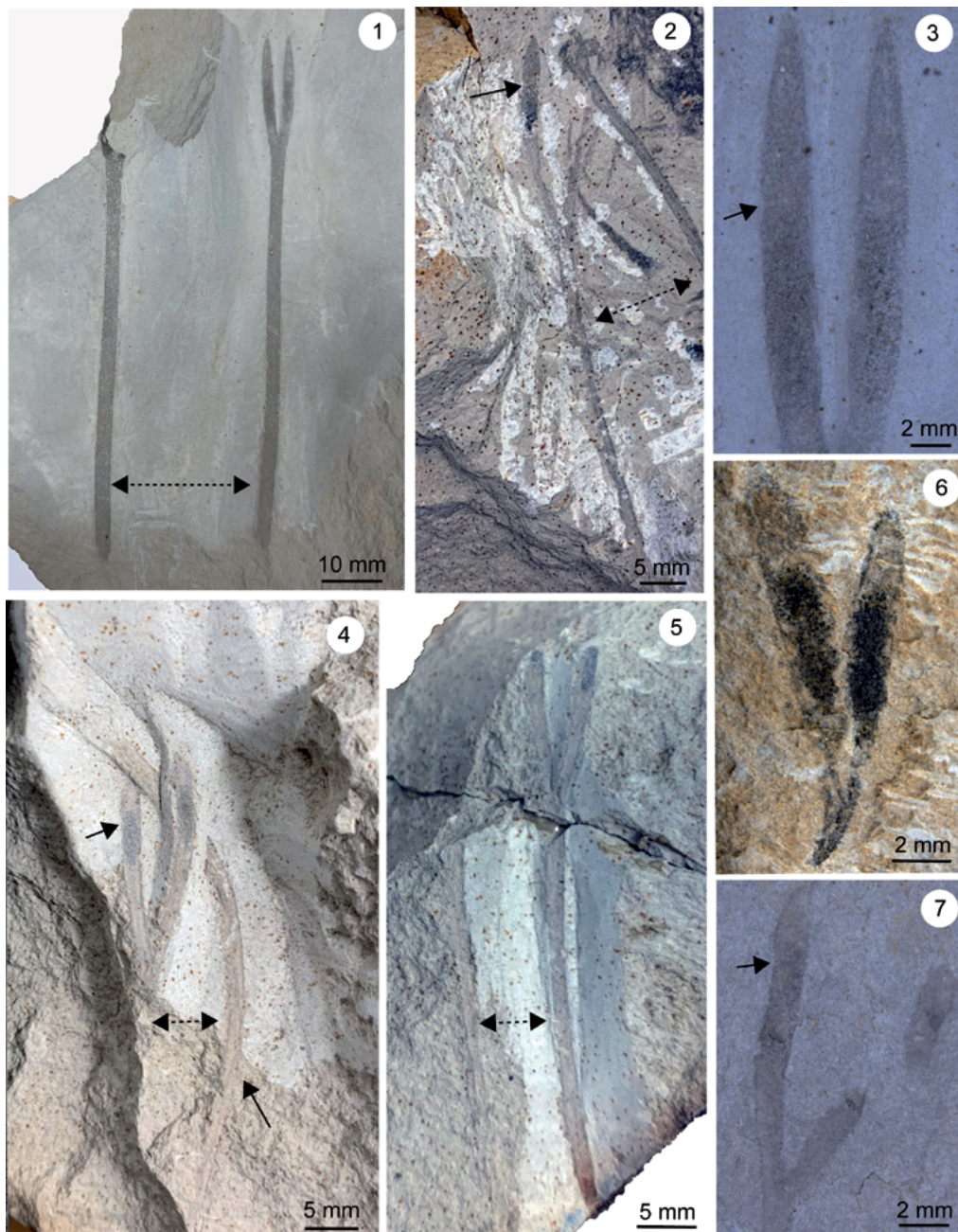
Figure 2. *Salopella australis* displaying parallel parent axes dichotomising into much shorter daughter axes that are terminated with elongate sporangia, delineated with a constriction just above dark sporogeneous region. All from Wilson Creek Shale on Frenchmans Spur track, 10 km west of Matlock. A, erect parent axes parallel to each other, dichotomising into two elongate sporangia from Wilson Creek Shale. Re-photographed here; originally published in Tims and Chambers (1984: pl. 32, fig. 4) and Tims (1980: fig. 4.1.9). Specimen NMV P50014. B, forked dichotomy terminated by sporangia from Wilson Creek Shale. And to the right hand side of the forked axis is another long axis, which based on its orientation may also be part of the same plant. Constriction at arrow, lower arrow at dichotomy and double arrow at two aligned axes. Specimen NMV P33219. C, close-up of fructification in A, sporangia barely extend beyond the confines of their subtending axes, with slight constriction present above sporogeneous region (at arrow). Specimen NMV P50014. D, E, holotype, part and counterpart. On part, constriction at arrow in sporangium. On counterpart, both parent axes are parallel to each other (at dotted arrow). Re-photographed here, originally published in Tims and Chambers (1984: pl. 32, figs. 1, 2). Specimens NMV P50008.1 and NMV P50008.2, respectively. F, Gen. et sp. indet. – short daughter axes terminated in elongate sporangia. The cortex may be absent from subtending axes, with only the central line visible. The lack of cortex prevents assigning to *S. australis* as width of subtending axis to sporangial width is required. Originally photographed by Tims (1980: fig. 4.1.13). Specimen NMV P50010.2. G, *S. australis*, with two short daughter axes, with constriction at arrow of the sporangium, which is the same width as its subtending axis. Specimen NMV P202886.

Description. The new specimen's length is 135 mm and consists of two synchronous dichotomies with longer than wide sporangia terminating each axis. The naked slender axes are 0.8–1.8 mm wide, with the axial width decreasing equally after each dichotomy. The first dichotomy occurs c. 80 mm from the base of the fossil and c. 31 mm from the second dichotomy (fig. 4A at lower arrow). The subtending axes to the sporangia are 0.9–1.0 mm wide and 22–25 mm high with some slight variation in the width along all four axes and a slight narrower evident beneath sporangia three and four (fig. 4B, the subtending axis to sporangium four pinches slightly about 1 mm below the sporangium). The sporangia are fusiform 1.5–2.0 mm wide and 4.8–6.0 mm high with the subtending axis slightly widening into the base of each sporangium. The widest part of the sporangia occurs in the lowest quarter length, followed by a gentle tapering to rounded sporangial tips. A sporangial wall is evident primarily but is not confined to the basal parts of the sporangia measuring 0.2–0.3 mm wide and is continuous with the subtending axes. Sporangia two, three on the part and four on the counterpart possess what appears to be an infilled oval presumed sporogenous area, which are no greater than 1.2 mm wide and 1.5 mm high. Sporangium four on the counterpart shows a fine linear cavity 0.15 mm wide entering the base of the sporogenous area and sporangium three on the part shows similar but larger opening beneath the sporogenous area, and beneath this is a fine central axis 0.1 mm wide; beneath sporangium two on the subtending axis, this axis is 0.2 mm wide. Sporangium two (part) upper half possesses longitudinally oblique striations, 0.06–0.6 mm apart.

Remarks. Comparison to holotype. The new specimen measures 50 mm longer than the holotype (fig. 3), and its axial width is broadly in range with the holotype, which measures 1.1–1.9 mm wide according to Tims and Chambers (1984). What appears to be the widening of the parent axis in the specimen (fig. 4A) is where the first dichotomy occurs, with the two daughter axes aligned for 26 mm before diverging for the remaining 5 mm before the second dichotomy. From the holotype, the best examples of branching to compare to the specimen were found on the part specimen (right-hand side) with isotomous dichotomies subtending sporangia one–seven (fig. 3A, fig. 6D). Proximally on the axes ultimately terminate in sporangia one–seven show the axes emanating from a horizontal axis. This horizontal axis may represent part of a rhizomatous system or a distorted axis. Tims and Chambers (1984) appear to have considered this a dichotomy because no other part of the fossil would give three dichotomies. However, it is equivocal as to whether it is a distorted axis with a dichotomy. Nonetheless, the axes of the new specimen examined are noticeably less flexuous than the holotype; for example, on the holotype axes leading to sporangia eight and nine showing changes in orientation of about 45° in conjunction with the daughter axes of dichotomies occurring at 10° and 45°. These differences possibly represent differences in both current strength during deposition and the level of degradation of each of the plants. There is a noticeable variation in the distance between the ultimate branching points and sporangia in the holotype, from c. 6 mm as seen in sporangium 12, to c. 26 mm

for sporangium seven, and up to at least 57 mm for sporangium eight, where the presumed branching point is not visible. The axes decreased after each dichotomy, as noted by Tims and Chambers (1984), but with the specimen examined herein there is a much greater decrease in axial width after the first dichotomy. Examination of the holotype did reveal a slight narrowing in the subtending axes (fig. 3D–F) of most of the sporangia (Tims and Chambers 1984: pl. 34, fig. 3); this was observed beneath two of the sporangia on the specimen, but in both cases may be artefacts of preservation, and more specimens are required to confirm this character.

The size range of the sporangia in the holotype, 3.2–6.0 mm high and 1.3–2.0 mm wide (Tims and Chambers, 1984), is similar to the specimen examined herein, and both have a comparable average height to width ratio of 2.6 (Morris and Edwards, 2014: table 3) for the holotype and 3.2 herein. The holotype shows slight variation in the location of the widest point of the sporangia, occurring either in the lowest quarter (fig. 4F), like with NMV P235941 (fig. 4C) or midway (fig. 3D). The minor difference is possibly accounted for by the different types of preservation. The specimen NMV P23591 shows these sporangial bodies in semi-relief and indicate they were not flattened bodies. Furthermore, examination of sporangia of the specimen revealed an oval presumed sporogenous region in the basal part of the sporangia, which is also present on sporangium 13 of the holotype (fig. 3H). Tims and Chambers (1984: pl. 33, figs 3–4) noted that on sporangium 13 of the holotype it may either be a double sporangium or dissociation of the sporangial wall giving the appearance of a double sporangium. The evidence of a sporogenous area basally and relatively thick sporangial walls from the specimen examined herein (fig. 4B) suggests either a crushed sporangium or stage of senescence pertaining to dehiscence. Furthermore, some of the sporangia in the holotype have a darkened presumed sporogenous area completely filling insides of the sporangia (fig. D–F), which may have resulted from the breakdown of the wall holding the sporogenous area prior to fossilisation, as the sporogenous area occurs as a basal oval body on all sporangia of the specimen examined.

Tims and Chambers (1984: pl. 33, fig. 3) found central lines of 0.2 mm diameter throughout the specimen, one of which was beneath sporangium 13. On the specimen NMV P235941, the central line was found to connect to base of the sporogenous region (fig. 4B, C), which Tims and Chambers (1984) had postulated. Tims and Chambers (1984) noted some axes of the holotype to dichotomise (c. 6.0 mm) relatively close to the base of the sporangia (fig. 3C); however, this was not the case with NMV P235941.

The presence of longitudinal oblique striations on the upper half of sporangium two may reflect cell orientation and possible twisting as a means of dehiscence. Obliquely orientated cells in the sporangia have been recorded for some *S. allenii* and absent for *S. marcensis* (Fanning et al., 1992; Morris and Edwards, 2014), and throughout the entire sporangia and subtending axes of *Tortilicaulis* (Edwards et al., 1994). There was no indication of twisting found for the subtending axes of the specimens' sporangia, suggesting it may only affect the upper part of the
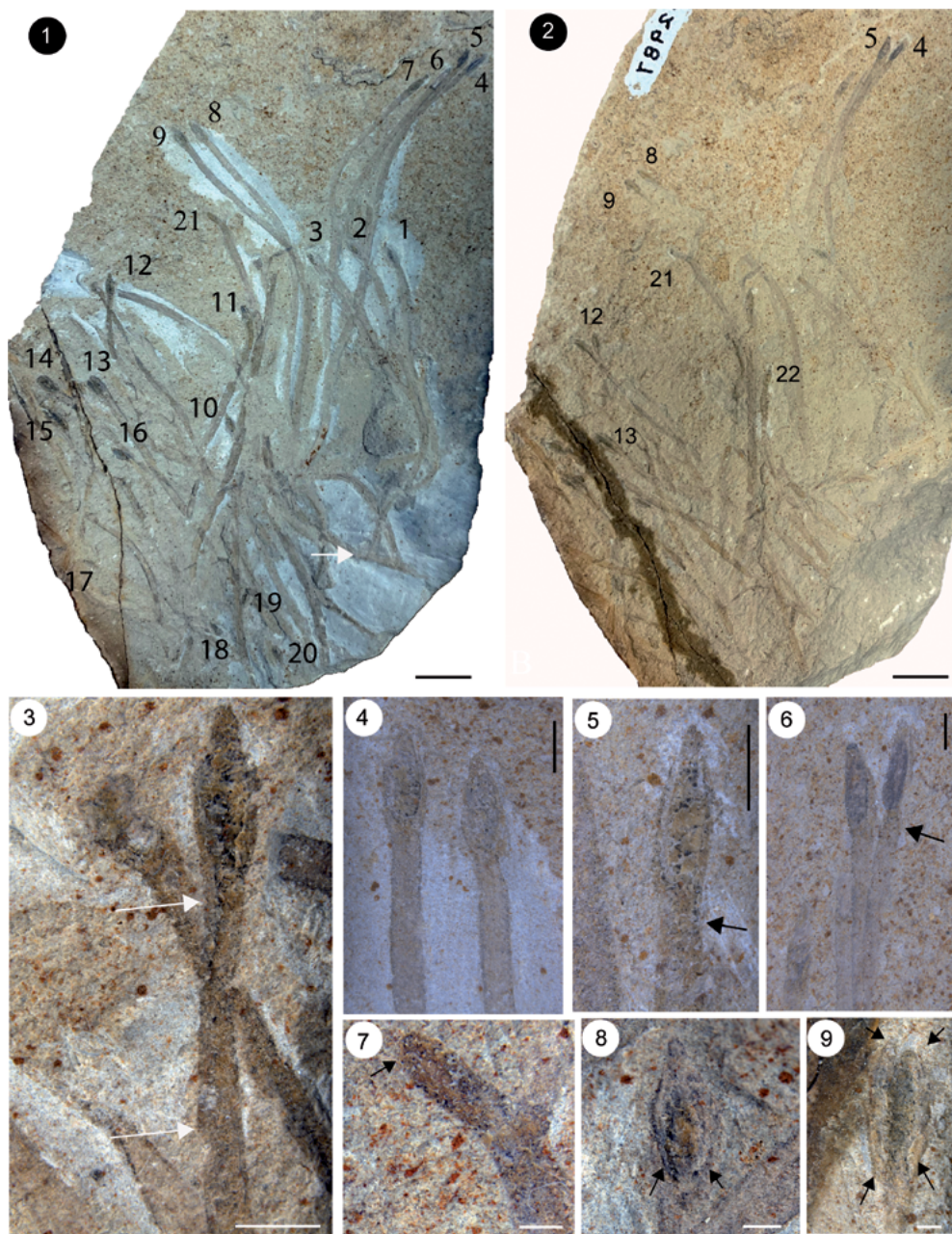
Figure 3. *Salopella caespitosa* (holotype) from Wilson Creek Shale on Frenchmans Spur track, 10 km west of Matlock. A, B, part (NMV P202987.1) and counterpart (NMV P202987.2), respectively; numbering follows Tims and Chambers (1984, pl. 33, fig. 1). Counterpart images are reversed to be in the same orientation as the part specimen. A, on right-hand side of part specimen, double isotomous dichotomies lead to sporangia one–seven. Note, at the arrows, there is perpendicular branching that is suggestive of a rhizomatous system. C, sporangium 12; at the arrow there is another axis that is terminated in a sporangium that is partially visible. Specimen NMV P202987.1. D–F, Evidence of a slight constriction beneath sporangia at arrows. D, sporangia eight and nine (on the left). Widest part of each sporangium occurring approximately midway along their length. Note, rephotographed; originally published in Tims and Chambers (1984: pl. 34, fig. 3). Specimen NMV P202987.1. E, sporangium 22 is c. 4.06 mm long and 1.4 mm wide. The axis decreases from 1.2 mm proximally to 0.5 mm just beneath the sporangium. Specimen = NMV P202987.2. F, sporangia four (right) and five, both sporangia are slightly wider in the lower quarter of each sporangia. Specimen = NMV P202987.2. G, sporangium 22, appears to be two immature sporangia juxtaposed. At arrow, the apex (rounded) of the smaller fusiform sporangium is apparent. Specimen NMV P202987.1. H, sporangium two, lower arrow at walls surrounding presumed oval sporogeneous area, which reaches approximately halfway the length of the sporangium to the upper arrow. Specimen NMV P202987.1. I, sporangium 13, arrows at walls surrounding sporangeneous area and upper arrow showing extent of oval sporogenous body. The walls does not recombine apically like in sporangium two, suggesting it may have been crushed, or hidden, beneath the matrix. Rephotographed; originally figured by Tims and Chambers (1984: pl. 33, fig. 3). Specimen NMV P202987.2.

sporangia; however, this is conjectural. As noted by Morris and Edwards (2014: 42), sporangia containing spores are required for unequivocal identification and assessment of relationships. While the specimen described is three-dimensionally preserved, we believe erecting a new taxon to segregate it from the form genus would be premature and we should wait for more data. The presence of this specimen at the base of the Humevale Formation potentially suggests a late Silurian age (Rickards, 2000). However, as outlined in the stratigraphy section, we suggest a Lower Devonian age range for specimens found at Ghin Ghin Road until unequivocal evidence of age becomes available.
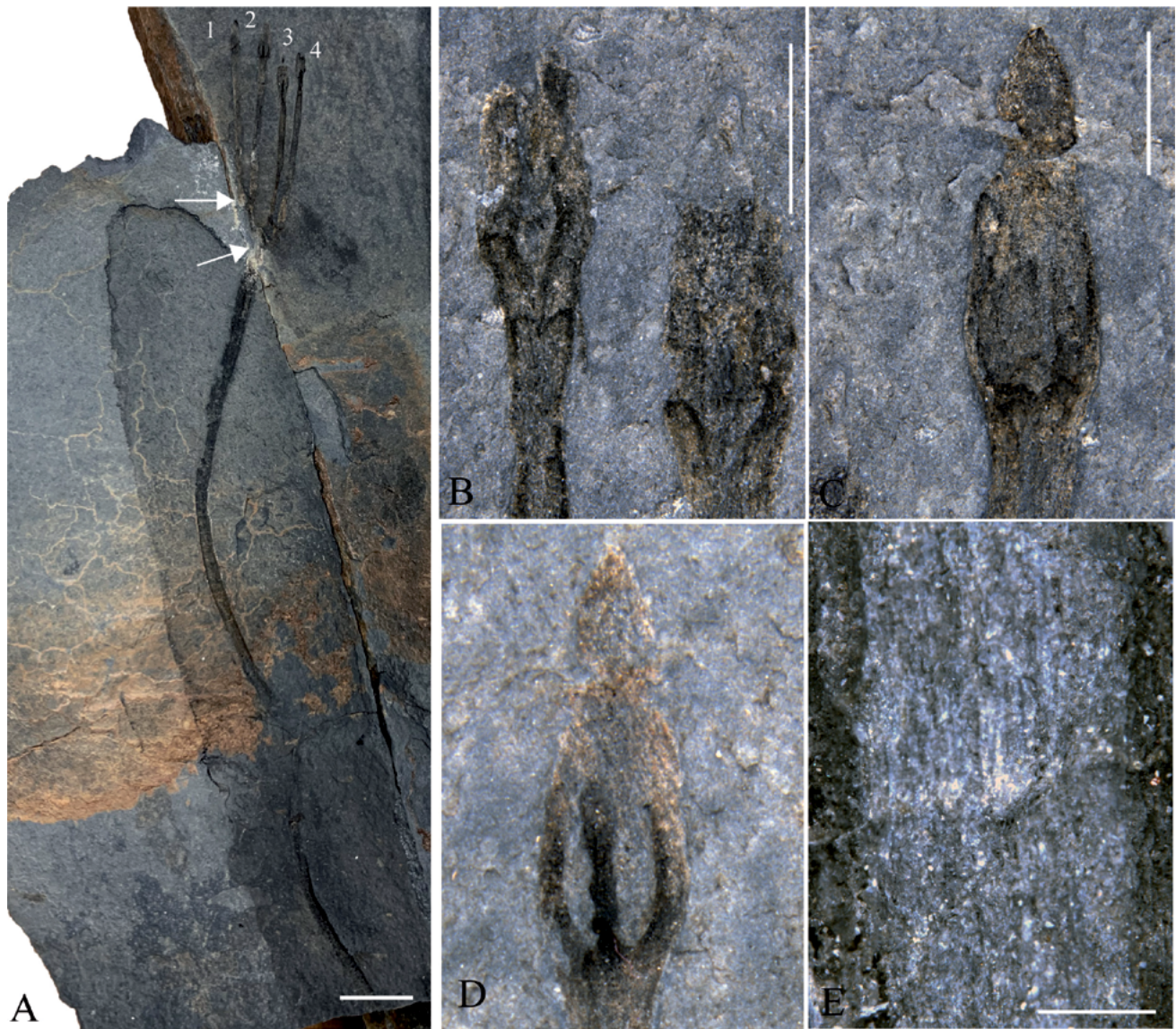

Figure 4. *Salopella caespitosa* NMV P235941 from Devil's Elbow on Ghin Ghin Road, northwest of Yea. A, overview of whole specimen. NMV P235941.1. B, arrow (Vt) at vascular trace entering base of oval presumed sporogenous body of sporangium four, and the subtending axis to sporangium four pinches slightly about 1 mm below the sporangium. Lower arrow at region where subtending axis is continuous with sporangial wall and upper arrow shows extent of sporangial body of sporangium three. Note, for both sporangia, the distal parts appear to be hidden in the matrix. NMV P235941.2. C, lower arrow (Vt) at vascular trace entering base of oval sporogenous body, with upper arrow at distal extent of sporogenous body on sporangium two on the counterpart. Note, no longitudinally oblique striations are evident in upper half of sporangium but are evident on the part specimen. NMV P235941.2. D, sporangium two at arrow longitudinal oblique striations on the upper half of the sporangium. NMV P235941.1. E, close-up of parent axis with longitudinal striations. NMV P235941.1.

Plantae. *Incertae sedis*

Genus. *Salopella* **Edwards and Richardson, 1974**

Salopella laidae McSweeney, Shimeta and Buckeridge, sp. nov. (fig. 5A, B, fig. 6D)
Salopella australis Tims and Chambers (1984: pl. 32, fig. 3, text-fig. 2C)

Diagnosis. Plant at least 55 mm long, tuft branching architecture, with sporangia all reaching the same height, with naked dichotomously synchronous branched axes up to 3.2 mm wide basally and 1.3 mm below sporangia. Axial width decreases after each dichotomy. Isotomous branching angles small, 30°–40° for the ultimate dichotomies and 15°–50° for basal dichotomies. At least two orders of branching. Branching 10.0–14.0 mm below sporangia. Eight sporangia, elongate sub-fusiform 9.7–11.0 mm high and up to 2.5 mm at widest section in mid region, and wider than subtending axes, obtuse apices.

Etymology. Named for Mrs Peg Laid who kindly gave permission to collect fossil specimens from her property on Ghin Ghin Road, Yea.

Holotype. NMV P50011.1 and NMV P50011.2, part and counterpart respectively, figured by Tims and Chambers, 1984: pl. 32, fig. 3 and text-fig. 2C

Locality. Location 4, Brackley's cutting (Harris and Thomas, 1941) Limestone Road, 2 km southeast of Yea. Note: exposure referred to as locality 62 in Couper (1965). 37° 12.38' S, 145° 25.39' E.

Stratigraphy and age. Location 4 (Harris and Thomas, 1941: 303) Yea Formation (Garratt 1978), Lower Devonian (Pragian; Edwards et al., 1997; Rickards, 2000; Rickards and Garratt, 1990).

Salopella laidae sp. nov. **(fig. 5A, B, fig. 6C)**

Description. Specimen preserved as a faint white compression on blue-grey claystone with six of the eight sporangia preserved. There is no clear sporogenous area within the sporangia. However, sporangia five, seven and eight (fig. 6C) on the part (fig. 5A) possess darkened creamy-grey regions extending up two-thirds of their lengths and possibly represent a sporogeneous region. No internal anatomy or spores were
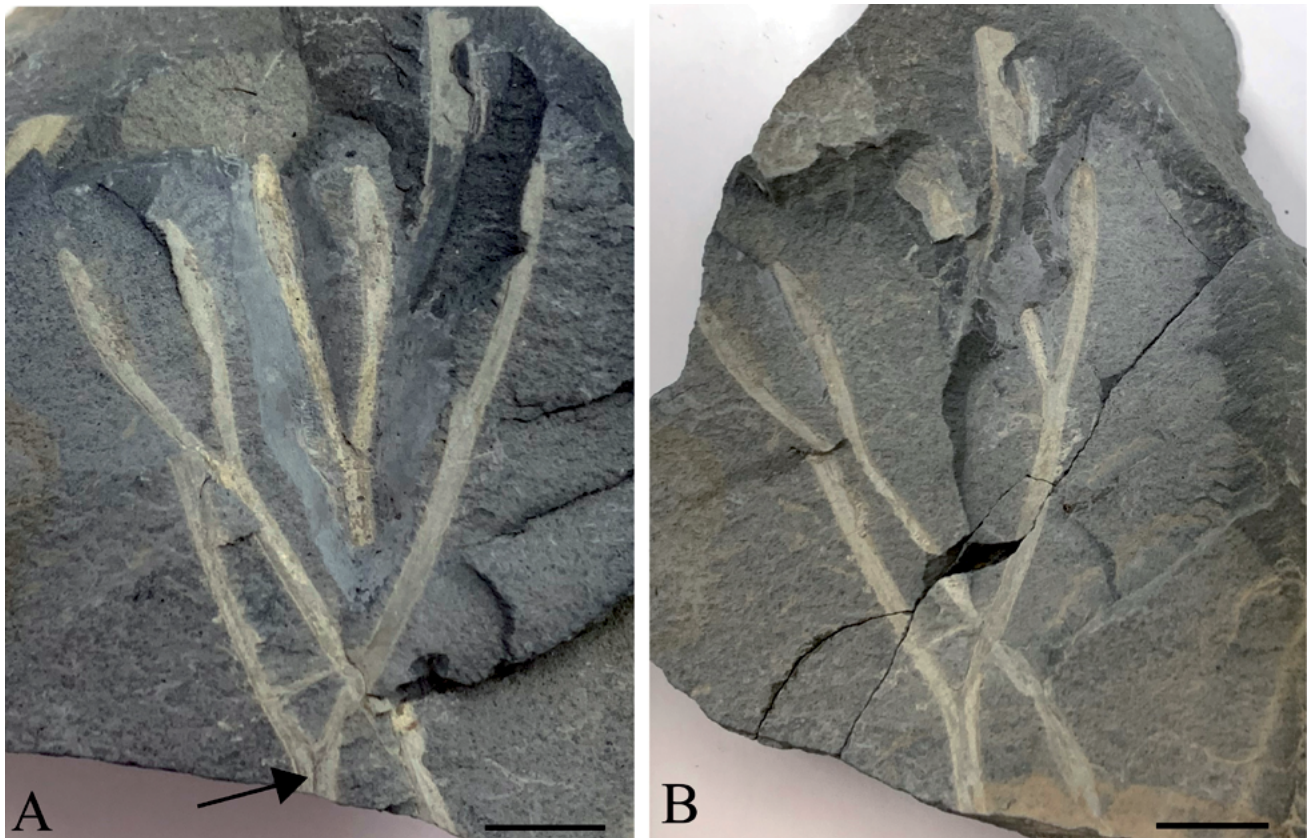

Figure 5. *Salopella laidae* sp. nov. (holotype) NMV P50011.1 and NMV P50011.2, part and counterpart, respectively, with counterpart reversed to be in the same orientation as part specimen. From location 4 (Brackley's cutting) on Limestone Road, Yea. A, double isotomous dichotomy visible, terminated with eight elongate sporangia, five visible. At lower arrow central line and at F, folding of tissue. On sporangium seven ?sporogenous region highlighted. Rephotographed; originally figured by Tims and Chambers, 1984: pl. 32, fig. 3 and text-fig. 2C. B, arrow at daughter axis missing on part present.

recovered when Tims and Chambers (1984) examined this specimen. The sporangia are slightly wider than the widths of their subtending axes and do not taper distally but come to a rounded apical region. There are two synchronous dichotomies clearly visible, with the axial width decreasing only after each dichotomy. Folding of tissue appearing as a longitudinal lineation along the edges of the axes and sporangia are visible; no evidence of dehiscence mechanism is present (fig. 5A).

Comments and comparison with other species. The diagnosis and description of this taxon is based on one specimen (part and counterpart). While we are mindful of issues in naming a new species on one specimen, we have done so because of the shape of the sporangia and compact branching architecture that set it apart from other rhyniophytoids (Table 1). The use of the paraphyletic genus *Salopella* (Edwards et al., 1994) is to emphasise its gross morphology and to follow previous workers (Tims and Chambers, 1984) in identifying Victorian flora. However, we note that work done by Edwards et al. (1994) on in situ *Salopella* spores demonstrated significant diversity, that can be difficult to ascertain because of convergence of some sporangial shapes (Edwards et al. 2001: 11), making assertions on palaeogeographic distribution and spread unwise without palynological evidence. Tims and Chambers (1984) originally assigned this specimen to *S. australis*, but *Salopella laidae* sp. nov. differs to *S. australis* in a number of its characters (fig. 6 – comparative line drawings of Australian *Salopella*). *Salopella laidae* sp. nov. possesses sporangia that are clearly delineated from their subtending axes, differing noticeably from coeval *S. australis* (fig. 2A–E) where the sporangia are as wide as their

subtending axes. Furthermore, the sporangia in *S. laidae* sp. nov. do not taper from half-way to one-third from their apices as in *S. australis*; instead, they hold their sporangial widths before terminating with rounded apices. While the sporangial apices appear obtuse, this cannot be assumed to have been the case in life, as Morris and Edwards (2014: 40) found when examining *S. allenii* that compressed specimens possessed rounded apices of varying degrees, except that one specimen of *S. allenii* that was preserved in 3D had a pointed apex. The parent axes leading to the ultimate dichotomy in *S. australis* are long, erect and aligned parallel to each other (fig. 2A), being easily distinguished from *S. laidae*, where the axes leading to the ultimate dichotomy are at an angle to the vertical. Furthermore, *S. australis* only possesses one dichotomy, while *S. laidae* possesses two, or possibly three, as suggested in Tims and Chambers (1984: text-fig. 2C). However, it should be noted the proximal axes of *S. laidae* sp. nov. are orientated away from each other, suggesting they may have come from a rhizomatous axis instead of a dichotomising one.

One of the parent axes of *S. laidae* sp. nov. is incomplete, but likely possessed four sporangia (fig. 6C). This is based on the relative dimensions, orientation and positions of both parent axes to each other, and that four sporangia terminate the daughter axes of the other parent axis.

The sporangia of *Salopella caespitosa* are ovate to fusiform and up to 6.0 mm high and 2.0 mm wide (Tims and Chambers, 1984), which is approximately half as high than *S. laidae*. Furthermore, the axes of *S. caespitosa* are more gracile than those of *S. laidae*, as the latter reached a maximum width of 1.9
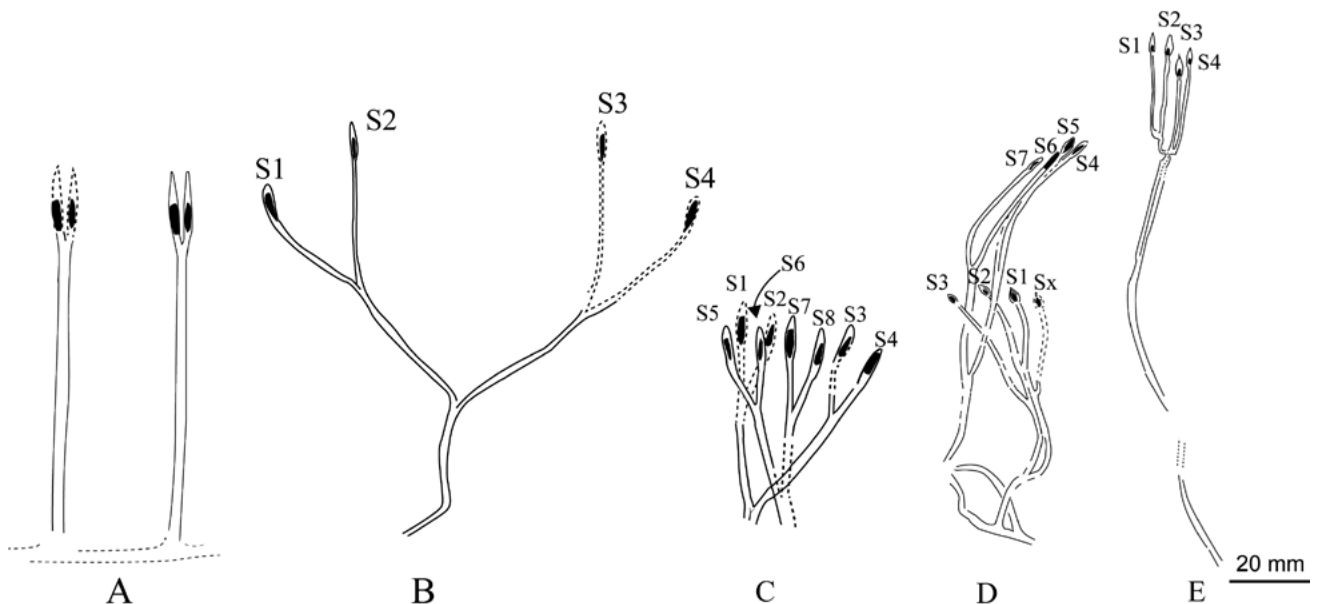

Figure 6. Line-drawings of Victorian early land plants with longer than wider sporangia. **A,** *Salopella australis* from Wilson Creek Shale on Frenchmans Spur track, near Matlock. Specimen NMV P50014. **B,** Gen. et sp. indet. from Limestone Road, Yea. Originally placed in *S. australis* but branching architecture clearly differs. Specimen NMV P157323. **C,** *Salopella laidae* sp. nov. from Limestone Road, Yea. NMV P50011. **D,** *Salopella caespitosa* (holotype) from Wilson Creek Shale on Frenchmans Spur track, near Matlock. Specimen NMV P202987. **E,** *Salopella caespitosa* from Ghin Ghin Road, Yea. Specimen NMV P235941.

mm proximally and 1 mm beneath the sporangia, whereas for *S. laidae* axes were at least 3.2 mm proximally and 1.3 mm beneath the sporangia. In comparison to other *Salopella* globally, the sporangia of *S. marcensis* and *S. xinjiangensis* are much smaller than *S. laidae*, reaching a maximum length of 3.4 mm and 3.5 mm long, respectively, and both much narrower (Morris and Edwards, 2014: table 3). Moreover, the sporangia of *S. xinjiangensis* are tongue-shaped (Cai et al., 1993; Dou and Sun, 1983), but *S. marcensis* sporangia are similar in gross morphology to *S. laidae*, being elongate and tapered at their apices according to Fanning et al. (1992). *Salopella marcensis* are much smaller plant than *S. laidae*, reaching 6.38 mm high, while *S. laidae* reached at least 55 mm high (Fanning et al., 1992: 174). While disarticulation for *S. marcensis* during transport seems likely, the isotomously branched axes bearing the sporangia for *S. marcensis* are much smaller than for *S. laidae*, ranging 0.05–0.5 mm wide (Fanning et al., 1992).

In Fanning et al. (1992: fig. 35), there is a silhouette of *S. marcensis* that shows a sporangium occurring on a lateral axis below a further bifurcation, indicating in this case at least that sporangia did not necessarily occur at approximately the same level, as is the case with *S. laidae* sp. nov. Finally, the type species of *Salopella*, *S. allenii* possessed fusiform or spear-shaped sporangia (Edwards and Richardson, 1974; Morris and Edwards, 2014) – significantly different to those of *S. laidae* sp. nov.

Discussion

Edwards and Richardson (1974) established *Salopella* based on one Lochkovian specimen of *Salopella allenii* from Brown Clee Hill, Shropshire (England); they noted its affinities to Rhyniaceae and that *S. allenii* possessed axes with dimensions that were between the range seen for *Rhynia gwynne-vaughani* and *R. major* (= *Aglaophyton majus*), with sporangia similar to both but lacking internal anatomy as seen in the Rhynie chert specimens (Edwards et al., 2017). Various workers have hypothesised that rhyniophytes/rhyniophytoids occupied ephemeral ruderal terranes, such as wetlands and deltas, whereby the rhyniophytes/rhyniophytoids completed their life cycles over short periods (Edwards, 2003; Edwards and Davies, 1990; Morris et al., 2011; Raymond et al., 2006; Wellman et al., 2000), possibly with some forming dense monotypic stands, such as the well-preserved aligned axes found near a fossilised channel from the Lower Old Red Sandstone deposits of Brecon Beacons (Edwards and Fanning, 1985: 156). According to Lavender and Wellman (2002), Edwards and Richardson (2004), and Raymond et al. (2006), seasonal conditions would have suited the short life cycles of rhyniophytes/rhyniophytoids. The location of the Melbourne Zone c. 30° south of the equator during the Lower Devonian (Torsvik and Cocks, 2019: fig. 9) suggests that the terrestrial sources for these deposits were likely also influenced by a seasonal climate, suiting the short life cycle of rhyniophyte/rhyniophytoids.

Furthermore, Edwards and Richardson (2004), when investigating the Lower Devonian calcrete palaeosols on the Avalonian Terrane, proposed rhyniophytes/rhyniophytoids as likely pioneer taxa because they were found on calcrete palaeosols that had formed in unstable interfluvial areas, with more advanced coeval plants, such as the zosterophylls or lycopsids, inhabiting more stable terranes to better accommodate their longer life cycles (Wellman et al., 2000). According to Powell et al. (2003: 29), there was a gradual shallowing of marine facies from the western margins of the Melbourne Zone in the Darraweit Guim Province, and eastward movement of the shoreline during the upper Silurian–Lower Devonian, which may have provided similar unstable conditions for rhyniophytes/rhyniophytoids, because palaeocurrents at areas in Yea and Matlock indicate a west or southwesterly source from the western parts of Victoria, which was terrestrial at the time (Powell et al., 2003: 23). Edwards and Davies (1990: fig. 16.3) noted the decline of rhyniophytes/rhyniophytoids from Laurussian sites during the late Pragian and Emsian stages of the Lower Devonian, possibly due to the proliferation of zosterophylls early in the Devonian. It is possible the uplift of the Tabberaberan highlands towards the end of the Lower Devonian in Victoria (Powell et al., 2003: 32) may have provided ideal unstable conditions for rhyniophytes/rhyniophytoids into the Emsian but work on the palaeoflora from the Norton Gully Sandstone Formation has been limited.

Finally, there is a noticeable difference in the number of rhyniophyte/rhyniophytoid taxa from Yunnan, China, in what was once part of the South China Block located at and north of the equator during the Lower Devonian (Torsvik and Cocks, 2019: fig. 9a), and those found in the *Baragwanathia* floral assemblage. According to Hao and Xue (2013: fig. 5.3), rhyniophytes/rhyniophytoids make up a small percentage (c. 2.7%) of the taxonomic groups found in the Posongchong Flora. Recently, Edwards and Li (2018b) erected *Polycladophyton gracilis* and *Jiangyounia gengi* possessing a grade of organisation belonging to Rhyniophytina. However, *Salopella* specimens have not yet been recovered (Hao and Xue, 2013: 193), suggestive of some level of isolation between the two regions.

Conclusions

Defining taxa based on gross morphological characters alone has limitations because it excludes cryptic characteristics and likely results in one morphospecies encompassing a number of distinct species. However, this study and the work of Tims and Chambers (1984) has provided a morphological framework from which new Victorian taxa may be defined, providing an impetus for further research.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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