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Lower Devonian *Zosterophyllum*-like plants from central Victoria, Australia, and their significance

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Abstract

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Three specimens belonging to Zosterophyllaceae are described. Two of these possess bilateral symmetry and are the first to be described with this arrangement from the Lower Devonian of Victoria. One of these specimens is similar to *Zosterophyllum fertile,* and the other cf. *Zosterophyllum* sp. A. is unusual in possessing vascularised long stalks. The third specimen described cf. *Zosterophyllum* sp. B. from Ghin Ghin Road, near Yea possesses a small spike and has sporangia that appear vertically elliptical and similar to some South China taxa. All the specimens are significantly different to previous zosterophyll taxa described from Victoria.

Keywords Victoria, *Baragwanathia* flora, *Platyzosterophyllum*, zosterophyll, systematics.

Introduction

The Wilson Creek Shale Formation of Victoria is notable for providing a link between the lithologies of the Mount Easton and Darraweit Guim Provinces (fig. 1) of the Melbourne Zone (VandenBerg, 1988: 114) and for being the type formation of *Baragwanathia longifolia* Lang and Cookson, 1935. Furthermore, it provides a useful approximate marker delineating the Silurian from Devonian rocks, as it has been dated as mid Pragian–Emsian (Carey and Bolger, 1995; Mawson and Talent, 1994). This paper examines three zosterophylls, two of which come from the Wilson Creek Shale and are the first to be described with bilateral symmetry in Victoria and are the first to be described from this formation. The third specimen is from the base of the Humevale Formation near Yea.

The first zosterophyll described from Victoria was *Zosterophyllum australianum* Lang and Cookson, 1930, from the Centennial Beds at North Road Quarry near Walhalla, now considered to be part of the Norton Gully Sandstone Formation (Douglas and Jell, 1985: 161). Lang and Cooksons' (1930: 148) work on *Z. australianum* confirmed an earlier assumption (Lang, 1927: 449–450) that the reinform appendages of *Zosterophyllum* were sporangia, with the presence of in situ spores. Additionally, Cookson (1935: pl. 10, figs 9–15) described *Z. australianum* from Mount Pleasant and Halls Flat Roads near Alexandra, also considered part of the Norton Gully Sandstone (VandenBerg, 1975, 1988). Hao and Wang (2000) reassigned Cookson's (1935) *Z. australianum* specimens to *Z. ramosum,* primarily based on different sporangial morphological characteristics. The *Zosterophyllum ramosum* type locality occurs near Zhichang village in the Posongchong Formation, Yunnan, China (Hao and Wang, 2000).

Tims (1980), in her unpublished thesis, described and gave informal manuscript names to three zosterophylls in Victoria: *Zosterophyllum minutum* from Boola Formation at Tyers, *Pluricaulis biformis* from the Yea Formation at Limestone Road and *Chamaecaulon tylosus* from the Wilson Creek Shale on Frenchmans Spur Track near Matlock. *Zosterophyllum minutum* was subsequently redescribed and assigned to *Gippslandites minutus* McSweeney et al., 2020. Additionally, McSweeney et al. (2020) described another zosterophyll, *Parazosterophyllum timsiae*, from the base of the Humevale formation on Ghin Ghin Road, Yea.

Stratigraphic setting

Humevale Siltstone. The Humevale Formation was proposed by Williams (1964: 277) as a sequence of primarily siltstones about 5 km south-west of Tommy's Hut at Humevale and is found throughout much of the Darraweit Guim Province (fig. 1) of the Melbourne Zone (Edwards et al., 1997: fig. 6; VandenBerg, 1988: table 4.1). Williams (1964) delineated the upper and lower parts of the Humevale Formation with two sandstone units: the Clonbinane and Flowerdale Members, respectively. Above the

Clonbinane Member near the base of the Humevale Formation, Williams (1964: 276) added the Mount Phillipa Member, a sandstone unit noted for numerous *Nucleospira* sp. and rhynchonellids. Garratt and Wright (1988: 650) subdivided the Humevale Formation based on brachiopod faunal successions, with *Notoparmella plentiensis* Garratt, 1980, above the base of the Humevale Formation in the Whittlesea area, and the appearance of *Boucotia janaea* Garratt, 1980, near the top of the sequence. However, Talent et al. (2001: 151) suggested *B. janaea* maybe *B. australis* Gill, 1942. Edwards et al. (1997: 22) considered the Clonbinane and Mount Phillipa Members to be part of the Dargile Formation, and the Flowerdale Member to be part of the Norton Gully Sandstone, while retaining the Humevale Siltstone. At Ghin Ghin Road, the fossil exposure P4 (loc 1 in Garratt, 1978) according to Rickards and Garratt (1990: fig. 2) is at the base of the Humevale Formation, and Pridoli, upper Silurian; thus, slightly younger than the exposure at Limestone Road, south-east of Yea, which they consider to be Ludlovian, with both interpretations based on graptolites. This Ludlovian–Pragian, upper Silurian age for the exposures in the Yea area by Garratt (1978), Rickards and Garratt (1990), and Rickards (2000) is contentious, primarily due to the relatively advanced plant architectures for this time and the similarity of some of the flora to younger exposures elsewhere in Victoria, such as the Wilson Creek Shale (Banks, 1980; Cleal and Thomas, 1999; Edwards et al., 1979 Hueber, 1983, 1992). Edwards et al. (1997: 22) placed much of the lithology of Yea, including both Limestone Road and Ghin Ghin Road exposures, in the lithologically variable Norton Gully Sandstone. VandenBerg (*pers. comm.* June 2021) mapped the Yea area in 2008 (unpublished) confirming much of Edwards et al. (1997), and found Yea to be predominantly Norton Gully Sandstone with a narrow band of the Wilson Creek Shale near the Yea anticline. In this paper, we retain the Humevale Siltstone, because this new information on the Yea lithology needs to be published. However, we find Edwards et al. (1997) and VandenBerg's argument cogent and so use a conservative interpretation of the age of the exposure at Ghin Ghin Road, giving it a Pragian–Emsian, Lower Devonian.

Wilson Creek Shale. The Wilson Creek Shale occurs in both the Darraweit Guim and Mount Easton provinces of the Melbourne Zone (fig. 1) and part of the Jordan River Group (VandenBerg, 1973, 1988). Lithologically, the Wilson Creek Shale consists of black shale that changes from cream to grey on weathering and is interpreted as representing once deep anoxic quiescent marine conditions (Edwards et al., 1997; VandenBerg et al., 2006). Sandstone beds are prevalent towards the top of the formation and are construed as representing the growing influence of turbidity currents late in the sequence (Edwards et al., 1997). Siltstone occurs primarily in the basal and upper portions of the formation, and limestone is found to interfinger with the Coopers Creek Formation at Jacobs Creek, north of Tyers (Edwards et al., 1997; VandenBerg, 1988; VandenBerg et al., 2006). The Wilson Creek Shale conformably overlies the Humevale Siltstones, Eldon Sandstone, Whitelaw Siltstone and Boola Formation, and conformably underlies the Norton Gully Sandstone, Easts Lookout Siltstone (fig. 2), Marshall Creek Member and Yeringberg Formation, albeit large scale strike faulting is common according to VandenBerg (1988) and VandenBerg et al. (2006). Lang and Cookson (1935) described – in addition to *Baragwanathia longifolia* – *Yarravia oblonga*, *Y. subsphaerica* and *Hostinella* sp. as occurring in the Wilson Creek Shale. Tims (1980) described numerous informal species in her thesis as occurring in the Wilson Creek Shale, especially at Frenchmans Spur Track and Coles Clearing on the Thomson River. Following her thesis, she described two rhyniophytoids, *Salopella australis* and *S. caespitosa*, and the trimerophyte *Dawsonites subarcuatus* as occurring in the Wilson Creek Shale at Frenchmans Spur Track, about 10 km west of Matlock (Tims and Chambers, 1984). Recently, *Salopella laidae* was described from Limestone Road by McSweeney et al. 2021c.

In the first half of the twentieth century, the lithological sequence that would be later assigned to the Wilson Creek Shale (Edwards et al., 1997; Thomas, 1953; VandenBerg, 1975, 2006) was believed to be early Ludlow, upper Silurian, based on Elles's assignation (Lang and Cookson, 1935: 422). Jaeger (1966) reassigned the graptolites to the Lower Devonian based on the occurrence of the monograptids *Uncinatograptus thomasi* (=*Monograptus thomasi thomasi*) Jaeger, 1966, throughout the formation, and *Neomonograptus notoaequabilis* (=*M. aequabilis notoaequabilis*) Jaeger and Stein, 1969, in the upper half of the formation (Lenz, 2013). *Neomonograptus notoaequabilis* extends into the overlying Norton Gully Sandstone according to VandenBerg et al. (2006). Furthermore, both *Eognathodus sulcatus sulcatus* and *Polynathus dehiscens* occur in the Coopers Creek Limestone that inter-fingers the Wilson Creek Shale at Tyers, indicating a mid Pragian–Emsian age (Carey and Bolger, 1995; Mawson and Talent, 1994).

Material and methods

The specimens cf. *Zosterophyllum* sp. A. (NMV P256740) and cf. *Z. fertile* (NMV P50040) were found by J. D. Tims on Frenchmans Spur Track near Matlock in the Wilson Creek Shale in the 1970s, with the former referred to in Tims (1980: fig. 4.4.19) indirectly, whereby she described three *Hedeia* (=*Yarravia*) sp., which occur on the same plane. Tims (1980) noted the specimen cf. *Zosterophyllum* sp. A. was loaned to H. P. Banks but made no reference to the associated zosterophyll. The specimen cf. *Zosterophyllum* sp. A. (McSweeney et al. 2021a) was given to the lead author by Prof. Dianne Edwards of Cardiff University in March 2019. The specimen cf. *Z. fertile* was originally assigned to *Zosterophyllum* sp. by Tims (1980: 91). The final specimen cf. *Zosterophyllum* sp. B. (NMV P256742) was found as float by the lead author at location P4 on Ghin Ghin Road, near Yea, on 8 August 2012, at location P4 on Ghin Ghin Road, about 8 km north north-west of Yea Township (37° 13' S, 145° 38' E). P4 is equivalent to loc. 1 in Garratt (1978: fig. 2).

Dégagement had been undertaken on cf. *Zosterophyllum* sp. A. to the right of the spike on the part. Further dégagement as per Fairon-Demaret et al. (1999) was carried out by the lead author to better expose sporangia two, four and five, and around the basal region of the fertile axis, and to expose part of the axis near the base and apex of the specimen. Samples taken from sporangia two and four of cf. *Zosterophyllum* sp. A. did not reveal any preserved spores, and samples of the basal axial region of the fertile axis did not yield any anatomical features when viewed under a low vacuum on a FEI Quanta 200 ESEM. Dégagement was performed on the distal and proximal parts of the spike of cf. *Z. fertile* by Tims (1980: 91) to expose sporangia in those areas, but no further dégagement was carried out because the specimen was fragile. Dégagement of cf. *Zosterophyllum* sp. B. was undertaken by the lead author around the spike, but no additional parts of the zosterophyll were found. A veneer of iron-oxide coating the surfaces was removed and mounted onto a stub and examined under a low vacuum on a FEI Quanta 200 ESEM. No spores or internal anatomy were uncovered.

Photographs of cf. *Zosterophyllum* sp. A., cf. *Z.* sp. B. and cf. *Z. fertile* were taken using a AxioCamMRc5 camera attached to a Zeiss microscope and a Leica M205 C microscope with Leica Application Suite software version 3.8.0. Images were Z-stacked to improve depth of field using Adobe Photoshop CC 2017. ImageJ software was used to take morphological measurements. Rodney Start of Museums Victoria took images of cf. *Zosterophyllum* sp. A. on 5 December 2019 using a Canon EOS 5D Mark III camera and cross-polarised light circular filter with flash strip-lights to enhance contrast. All photographs had contrast enhanced using Adobe Photoshop CC 2017 and were arranged using Adobe Illustrator CC 2017.

Institutional abbreviation

NMV P, Museum Victoria Palaeontology Collection, Melbourne, Australia

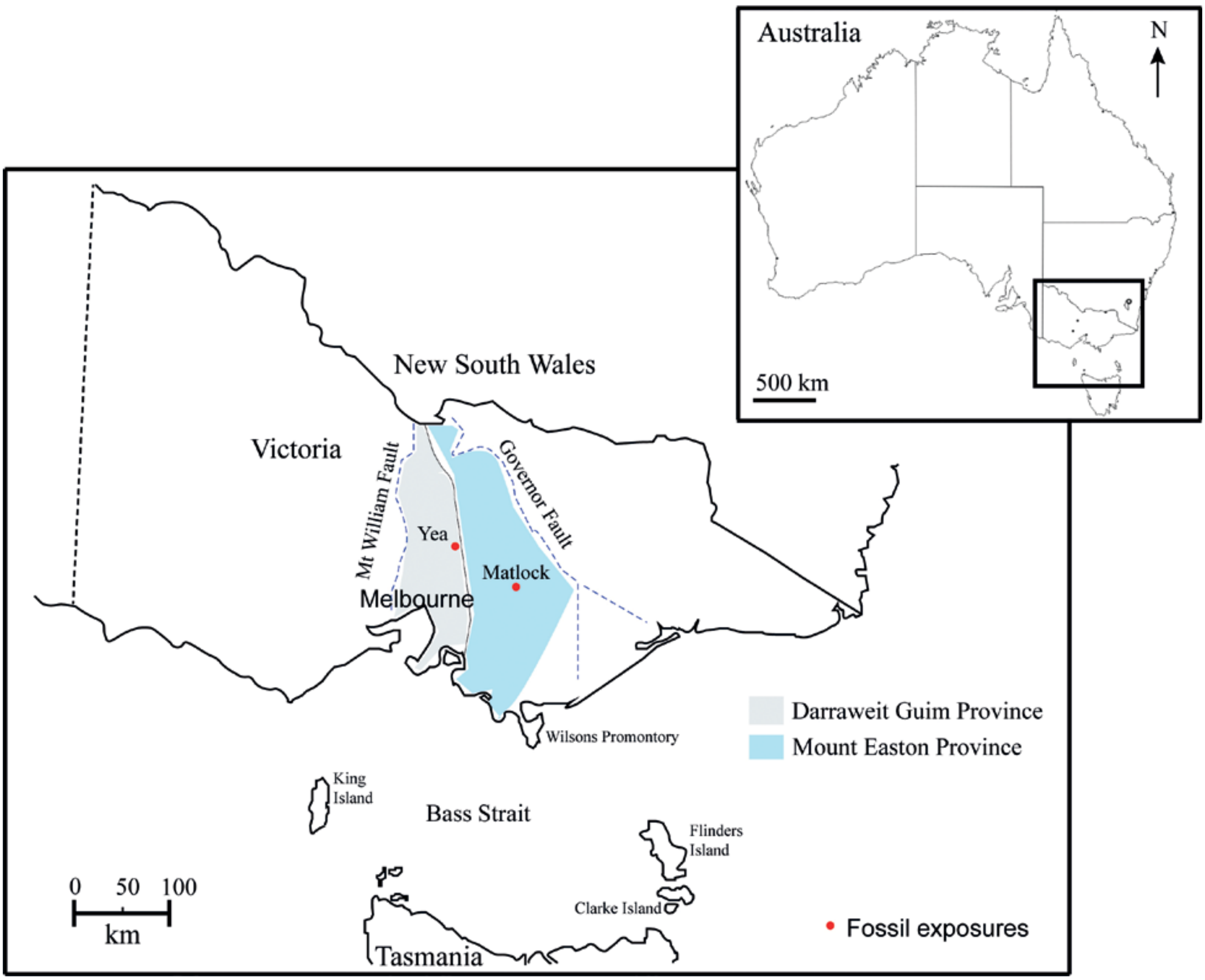

Figure 1. Location of Matlock in the Mount Easton Province and Yea in the Darraweit Guim Province of the Melbourne Zone in Victoria, Australia. Source: after Moore et al. (1998: fig. 2).

Systematic palaeontology

Division Tracheophyta

Class Zosterophyllopsida Hao and Xue, 2013

Order Zosterophyllales Banks, 1968

Family Zosterophyllaceae Banks, 1968

Remarks. Initially, *Zosterophyllum* were separated into two groups, *Platy-zosterophyllum* and *Eu-zosterophyllum*, by Croft and Lang (1942: 145), but Hueber (1972: 121) split *Zosterophyllum* into two subgenera, *Platyzosterophyllum* and *Zosterophyllum*. The distinguishing character of *Platyzosterophyllum* is the arrangement of sporangia in row(s) of one, two or three along the fertile axes, while the sporangia of *Zosterophyllum* are arranged helically (Croft and Lang, 1942; Edward, 1975; Gensel, 1982; Hueber, 1972). Furthermore, *Platyzosterophyllum* often possess circinate vernation (Croft and Lang, 1942; Edward, 1975; Gensel, 1982; Hueber, 1972). The specimens cf. *Zosterophyllum* sp. A. and cf. *Z. fertile* described herein possess bilateral symmetry, but lack enough characteristics to unequivocally assign to *Platyzosterophyllum*.

cf. *Zosterophyllum fertile* Leclercq, 1942

Figure 3a–c

Material examined. NMV P50040.1 and P50040.2, part and counterpart, respectively.

Locality. Occurs on a road cutting on Frenchmans Spur Track, approximately midway between Big River Road to the north-north-west, Warburton Road to the east and Frenchmans Spur Track, ~10 km west of Matlock, central Victoria.

Horizon and age. Wilson Creek Shale Formation, middle Pragian–Emsian, Lower Devonian (Carey and Bolger, 1995; Mawson and Talent, 1994).

Description. The specimen consists of part and counterpart of one partial spike with basal and apical regions missing and preserved as a carbonised compression. The axis is ~1.0 mm wide and 10.0 mm long and unbranched, and the spike up to 6.8 mm wide. Eight sporangia are borne alternately in two rows. The sporangia are attached by recurved stalks; some are perpendicular to ~60° to the fertile axis and curve sharply distally to at most 90°. The convex margins of some of the

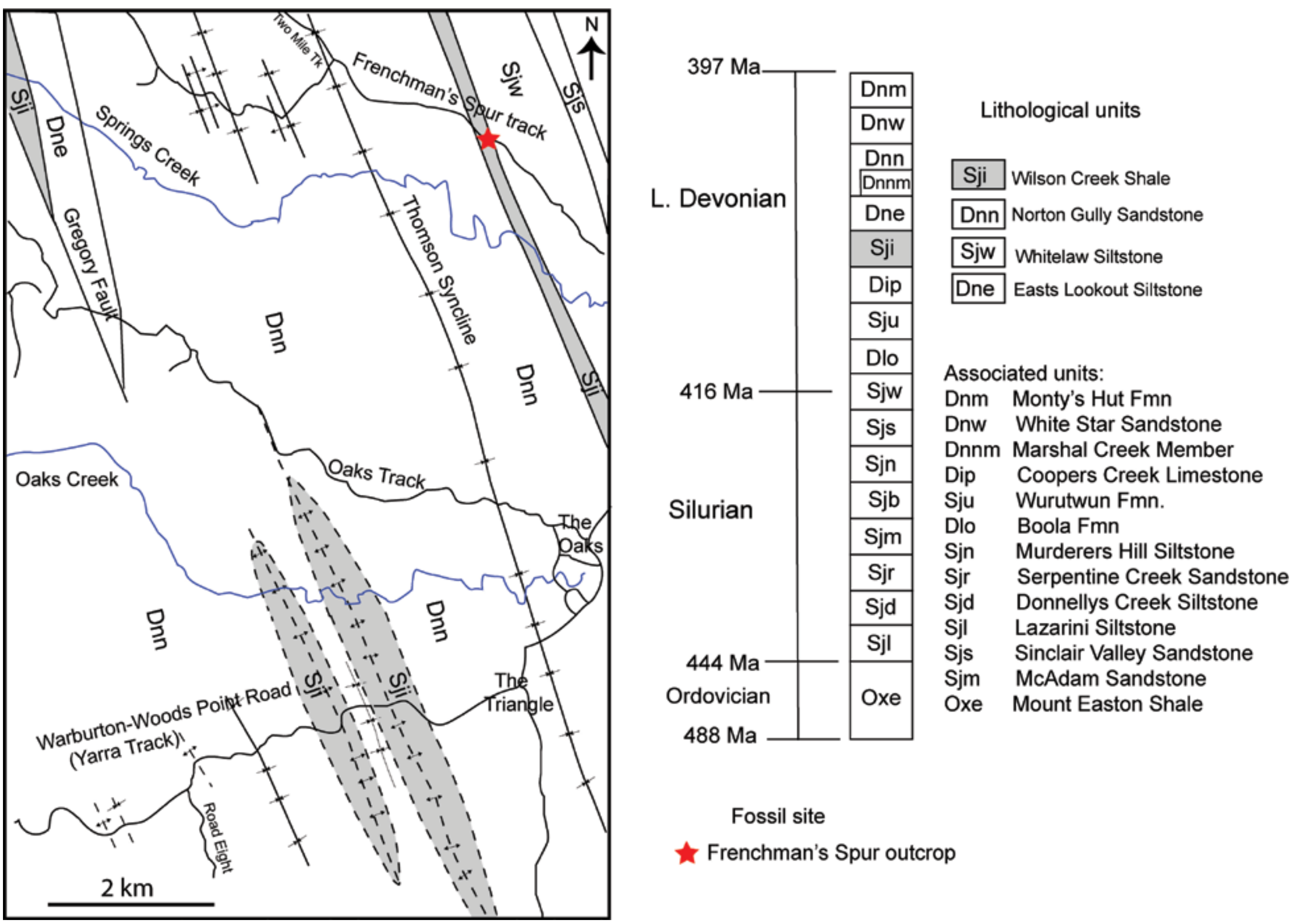

Figure 2. Location of the Wilson Creek Shale outcrop on Frenchmans Spur Track, 10 km west of Matlock. Geological map showing the location of Frenchmans Spur outcrop at the star, north of Springs Creek. Source: Map after Willman et al. (2006).

sporangia possess a thickened/darker/border, here interpreted as likely pertaining to dehiscence (fig. 3, sporangia 6, 7). An adaxially orientated basal lobe occurs on some sporangia (fig. 3b, central arrows).

Remarks. The sporangia are in two rows with no clear demarcation between the attachment of the stalk and the basal region of the sporangia. The specimen bears some resemblance to Edwards' (1969a: fig. 1b) South Wales *Z.* cf. *fertile*. Edwards' (1969a) specimens are from the Old Red Sandstone Brecon Beacons and Llanover Quarries, South Wales (Pragian–Emsian Lower Devonian age) and were placed in *Z.* cf. *fertile*, because the original diagnosis was based on only a single specimen from Belgium (Leclercq, 1942) such that further specimens from both Wales and Belgium were thought necessary to determine specific affinity with confidence. Wellman et al. (2000) recorded the earliest occurrence of *Z.* cf. *fertile* from the Anglo-Welsh Basin as being mid-Lochkovian (Lower Devonian). The fructification of Edwards' (1969a) specimens, while incomplete, were 1.0 cm high and 3.0 mm wide, which is comparable in height but over two times smaller than the Victorian specimen, which reached 6.8 mm wide. Edwards' (1972) *Z. fertile*, also based on an incomplete spike but with a significant proportion preserved, was 7.2 cm high and 3.0 mm wide, while Wellman et al.'s (2000) *Z.* cf. *fertile* reached 2.0 cm in height and 3.5 mm wide. Axial width for Leclercq's (1942) holotype measured 1.0–1.5 mm wide and conforms to the Victorian specimen. However, the Victorian specimen's axis, where visible, was found to be ~1.0 mm wide. The widest axial width for *Z. fertile* was found by Edwards (1972: 78) for a specimen from the Lower Old Red Sandstone of Forfar, Scotland, with an axial width of 3.0 mm, decreasing only slightly to 2.8 mm wide, while the specimens of *Z.* cf. *fertile* from Brecon Beacons Quarry, according to Edwards (1969a: 924), showed greater range, 0.8–2.5 mm wide.

The stalks for Leclercq (1942), Edwards (1969a, 1972) and Wellman et al. (2000) range between 0.3–0.5 mm wide and 1.0–1.8 mm long. The Victorian cf. *Z. fertile* stalks are broadly similar, 0.5–0.7 mm wide and up to ~2.0 mm long.

The sporangial shape in face view for the Victorian specimen is reniform (fig. 3, sporangium 8), similar to Wellman et al. (2000), while Leclercq (1942) described it as elongate–reniform, and Edwards (1969a) for *Z.* cf. *fertile* described it as irregular. The sporangia examined by Leclercq (1942), Edwards (1969a, 1972) and Wellman et al. (2000) were all in the range of 2.0–2.5 mm wide and 1.6–3.1 mm high. The sporangial dimensions of cf. *Z. fertile* are difficult to ascertain due to their poor preservation.

Edwards (1969a: 924) found the longest fructification of *Z.* cf. *fertile*. It had eight sporangia but lacked an apical region. Due to the lack of a complete spike herein and poor preservation resulting in equivocal characters, the Victorian specimen was placed in cf. *Z. fertile*, it being conceivable that given better preservation the plant might be placed it outside the defining characteristics of *Zosterophyllum*.

cf. *Zosterophyllum* sp. A

Gen. et sp. indet.

Figures 4–9

Material examined. NMV P256740.1 and P256740.2, part and counterpart, respectively.

Locality. Frenchmans Spur Track, ~10 km west of Matlock, central Victoria.

Horizon and age. Wilson Creek Shale, middle Pragian–Emsian, L. Devonian (Carey and Bolger, 1995; Mawson and Talent, 1994).

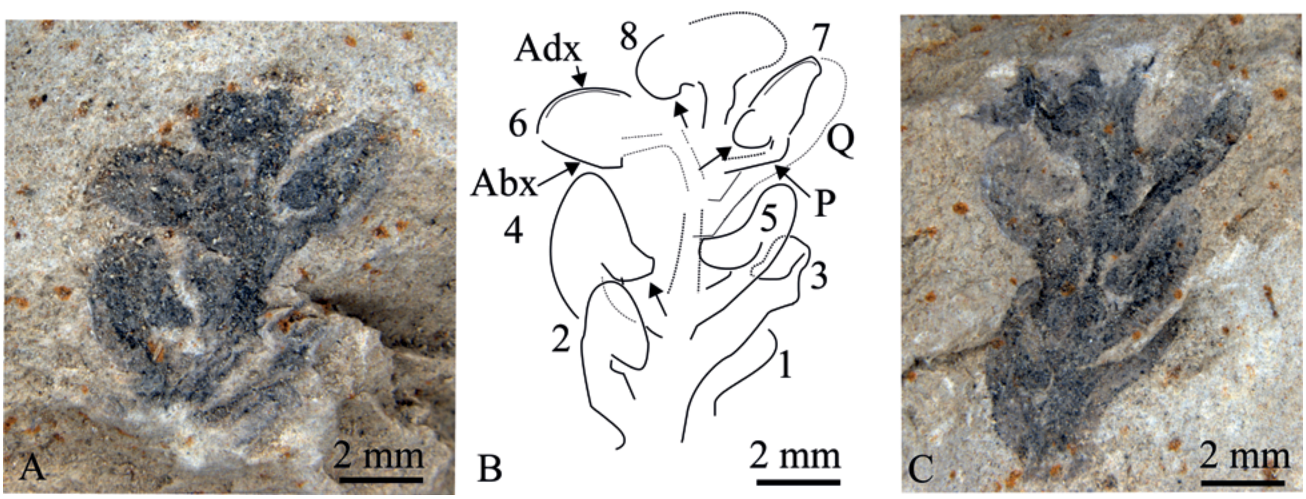

Figure 3. cf. *Z. fertile*, from the Wilson Creek Shale Formation on Frenchmans Spur, 10 km west of Matlock: a, part (NMV P50040.1); b, line drawing of partial spike. Abx = abaxial valve, Adx = adaxial valve, Q = ?poorly preserved sporangium, P = stalk, which is normal to the fertile axis before turning upwards. Central arrows pointing to lobes; c, counterpart (NMV P50040.2). Note. Counterpart image reversed to be in the same orientation as the part.

Description. The specimen consists of a longitudinally elongate lax spike with its apical region missing. The basal half of the spike contains about a third of the total sporangia in two rows (figs 4, 5a), and distally, the sporangia are more closely arranged (?helically) but the insertion points are not clear. The naked fertile axis is unbranched, 1.3–2.6 mm wide, curving basally, the spike slightly decreases in width acropetally. The lax spike is 10 mm wide and up to at least 45 mm long, consisting of 20 sporangia arranged on long vascularised stalks up to 2.0 mm long and 1.0–1.3 mm wide, at acute angles 15°–45° to the vertical, before the stalks reorientate towards the apex of the spike just beneath each sporangium. There is very little vertical overlap of sporangia. Some fine protuberances and depressions emanating from the vascular trace (fig. 6) are interpreted here as representing insertions of further stalks. The junction between sporangium and stalk is unknown. The sporangia are circular to reniform in face view, 0.95–3.7 mm wide and 0.5–2.3 mm high, with weakly developed lobes (fig. 7) and a narrow border visible on distal margin of some sporangia, such as sporangia two, 10 (figs 7, 8) and 12, are 0.13–0.15 mm wide and is interpreted as likely pertaining to dehiscence. Sporangia one and two are longitudinally elliptical and are interpreted to be infolded, such that half the abaxial valve is visible (fig. 8). Vascular trace 0.34–1.3 mm in the fertile axis, 0.17–0.21 mm on the stalks. There are two sporangia in close proximity to the spike, but they are clearly orientated at an angle to indicate they may come from another axis in their vicinity (fig. 5a).

The vascular trace is conspicuous in that it is preferentially preserved compared with cortical tissue (fig. 4), the cortex being preserved as a grey film in the surrounding matrix. The stalk of sporangium one (fig. 8) is inserted almost perpendicular to the fertile axis and is bent such that most of the stalk is parallel to the fertile axis before curving upwards, just beneath the basal region of the sporangium. Several poorly preserved axes lie

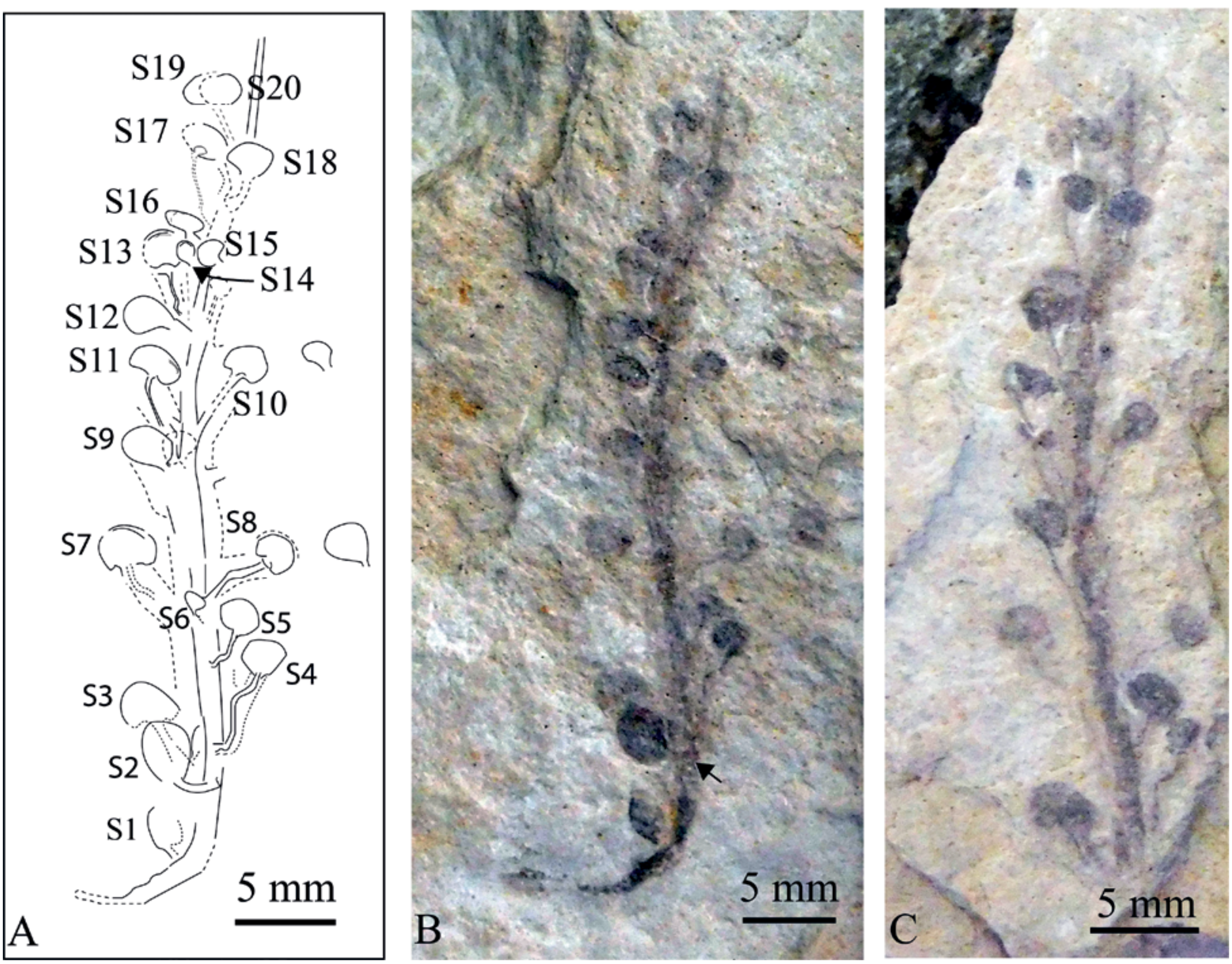

Figure 4. cf. *Zosterophyllum* sp. A. from the Wilson Creek Shale Formation on Frenchmans Spur, 10 km west of Matlock: a, line drawing, dotted lines are from faint remains of compression. S=Sporangium; Q=Poorly preserved sporangium or sporangium likely not belonging to same spike; b, part NMV P256740.1. Arrow at stalk, which has been pushed across fertile axis; c, counterpart, NMV P256740.2 with part of basal region of spike missing. Note. Counterpart image reversed to be in the same orientation as the part.

beneath the spike but are too poorly preserved and lack direct connection to warrant further consideration. However, the subtending axis to the spike aligns with an axis 4 mm wide (figs. 8, 9) and is suggestive of derivation from the same spike. This suggests the linear aerial extent of cover of the plant was at least 45 mm wide. Furthermore, the horizontal orientation of this axis to the spike is suggestive of a rhizomatous system, but it remains equivocal due to the absence of reticulum axes and H- and K-branching (*sensu* Hao et al., 2010: fig. 3; Walton, 1964: fig. 1). To the right of the apical region of the spike on the part, there are at least four axes that do not possess any attached sporangia, and beneath these axes towards the middle of the spike, a poorly preserved axis is visible with two sporangia (fig. 9) not directly attached to it but with their sporangial stalks orientated towards it, suggesting it was once attached. The alignment of these axes with the spike may indicate a tuft habit, but without clear evidence of additional spikes, its habit remains inexplicit.

Remarks. The description is based on one specimen – 45 mm high, part and counterpart with one spike (fig. 4) with sporangia laxly arranged on vascularised long stalks – preserved as a fine film of carbonaceous material lacking anatomy. The specimen occurs with three specimens of *Yarravia* sp. Lang and Cookson, 1935, on the same plane (McSweeney et al. 2021a: fig. 5a–d). The limits of the fertile axis and stalks are defined by grey film on each side of a much darker vascular trace. The fine slender nature of the darkened linear structures below the stalks are too narrow to support a sporangium, such that it seems parsimonious for the original widths of the axes to be defined by these ghosted grey areas. Lele and Walton (1961: 471), when describing axes prepared from acetate transfers, found the xylem to appear as a preferentially preserved dark bands (and to be about one sixth the axial width) and noted the vascular traces were often displaced from their central position. This, they postulated, was likely due to decay of the cortex prior to burial during early digenesis. This would help explain the convoluted nature of the vascular trace herein (figs. 4–6), indicating the structure of the axes had already started to break down before becoming fully fossilised.

The specimen possesses depressions and protuberances along parts of its fertile axis, which is especially noticeable midway along the spike (fig. 6). These are interpreted as likely insertion points for some axes of sporangia and follows Edwards' (1975: 255) interpretation of a similar feature on *Z. myretonianum*. Xue (2009: 507), in describing *Z. minorstachyum*, suggested that small conical protuberances along the axes may reflect parasitism. This possibility was considered, but the irregularities on the vascular trace are primarily depressions in areas noticeably lacking sporangia, and in some cases appear to be the basal-most attachment of the stalk to the fertile axis' vascular trace. Additionally, we did not consider areas lacking in sporangia to be indicative of a deciduous spike, as seen with *Z. deciduum* from the Emsian, Lower Devonian of Belgium (Gerrienne, 1988). While it is plausible that once the more mature proximal sporangia has dehisced and subsequently abscised, plants would be better served by losing some sporangia in this region to concentrate energy on immature sporangia in the distal region of the spike. However, the specimen still possesses large proximal sporangia and only some sporangia appear to be missing, suggesting that

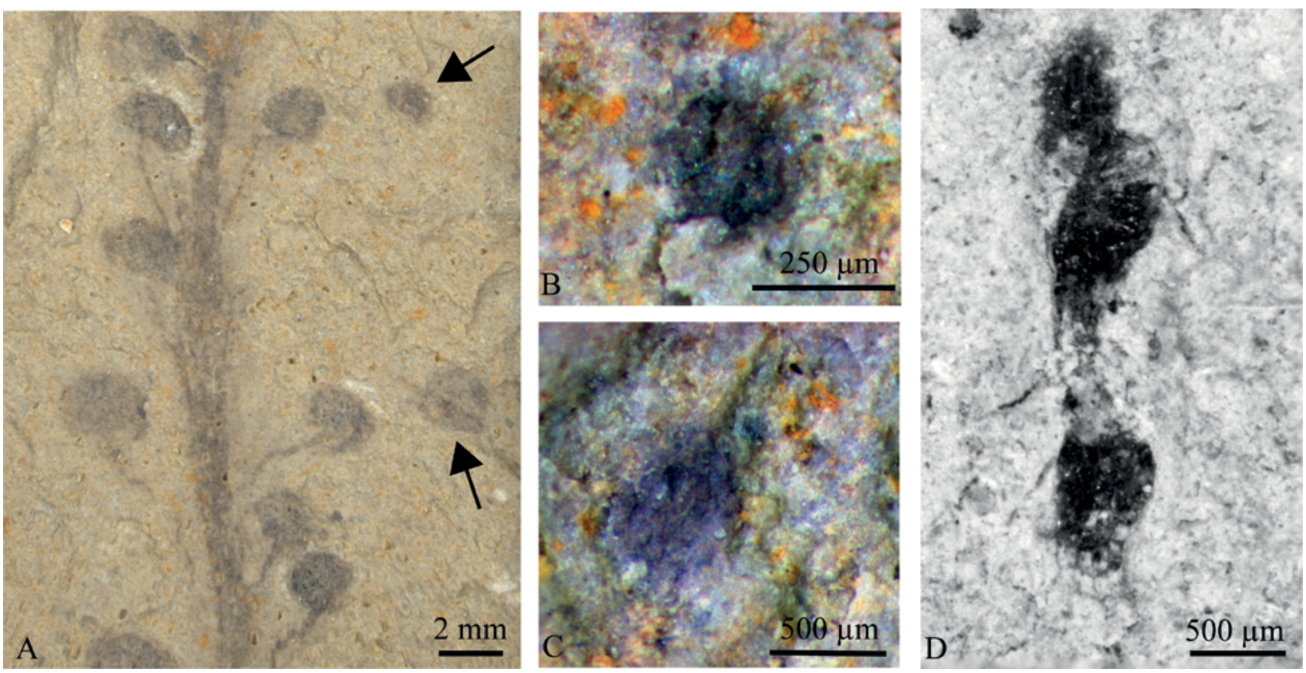

Figure 5. cf. *Zosterophyllum* sp. A. (part, NMV P256740.1): a, two isolated sporangia at arrows (pre-dégagement) with basal region of both sporangia orientated away from the spike; b–d, on the reverse of the slab, isolated sporangia with much similar dimensions and weakly developed sporangial lobes. Image a taken by Rodney Start © Museums Victoria.

they may have been lost, most likely as a result of excision due to the biostratinomy phase (Jackson, 2010: 5) of fossilisation. The absence of a junction at the axial–sporangial interface does not mean it never existed because it may have been destroyed during fossilisation. When examining Llanover specimens of *Zosterophyllum* from the Old Red Sandstone of South Wales, Edwards (1969a: 924) found organs could be superimposed and amalgamated into the surrounding tissue during preservation, resulting in them been indistinguishable.

The specimen described herein is atypical in comparison with most *Zosterophyllums* because of paucity of folded sporangia seen in lateral view with only two proximal sporangia so preserved. Furthermore, the sporangia rarely overlap each other, with one instance occurring in the proximal region of the spike where sporangium two has been pushed onto the basal region of sporangium three (fig. 4b, arrow at stalk of sporangium two) and distally for sporangia 19 and 20 (fig. 4).

Comparison with other taxa. The sporangia of the specimen are borne alternatively in two rows on opposite sides of the axis, akin to *Platyzosterophyllum*, and so the specimen was compared to *Platyzosterophyllum* first. However, some *Platyzosterophyllum* possess sporangia emanating from two rows on one side of the axis, such as *Z.* cf. *fertile* in Wellman et al. (2000: 181) and are noticeably more compact. The stalks of *Z. fertile* are perpendicular to the fertile axis, before sharply turning towards the apex, such that they are borne in an upright to slightly recumbent position (Wellman et al. 2000: 181). This characteristic of recurved stalks perpendicular to the fertile axis is also seen in *Z. spectabile* Schweitzer, 1979, according to Gensel (1982: 662). However, the specimen clearly differs from these taxa because the stalks are orientated at acute angles of 15°–45° without any noticeable change in orientation, other than immediately below each sporangium, where they sharply reorientate upright and parallel to the fertile axis (figs 5a, 6, 7a). Furthermore, the sporangia of *Z. fertile* are oblate (Wellman et al. 2000: 183), being almost linear along the margins, while the specimen's sporangia are rounded to reniform. The dimensions of both taxa also differ slightly, with *Z. fertile* possessing stalks that are much narrower than the 1.0–1.2 mm width for the specimen, with *Z. fertile* at most reaching 0.5 mm wide (Edwards, 1972) but generally (including for *Z.* cf. *fertile*) 0.3–0.4 mm wide (Edwards, 1969a; Leclercq, 1942; Wellman et al., 2000). The sporangial dimensions for *Z. fertile* are, in part, similar to the specimen, with the sporangia of *Z. fertile* up to 2.3 mm wide (Edwards, 1972), and for *Z.* cf. *fertile* specimens the sporangial dimensions were 2.0–2.3 mm wide (Edwards, 1969a; Leclercq, 1942; Wellman et al., 2000). The specimen's sporangial widths vary more greatly on the same spike and range between 0.95–3.7 mm wide, suggesting the plant was not mature. In comparison with the Welsh specimen, *Z. llanoveranum*, sporangia are arranged in 1–2 alternative rows but differs from the specimen with sporangia borne close together and in the distal region of the spike, sometimes helically arranged (Edwards, 1969b). This could not be confirmed here because the stalk insertion points are lacking.

Edwards (1975: 263) cautioned against the use of the arrangement of the sporangia on the spike as a definitive characteristic with which to delineate species. Edwards noted bilateral symmetry basally in the spike with the distal part

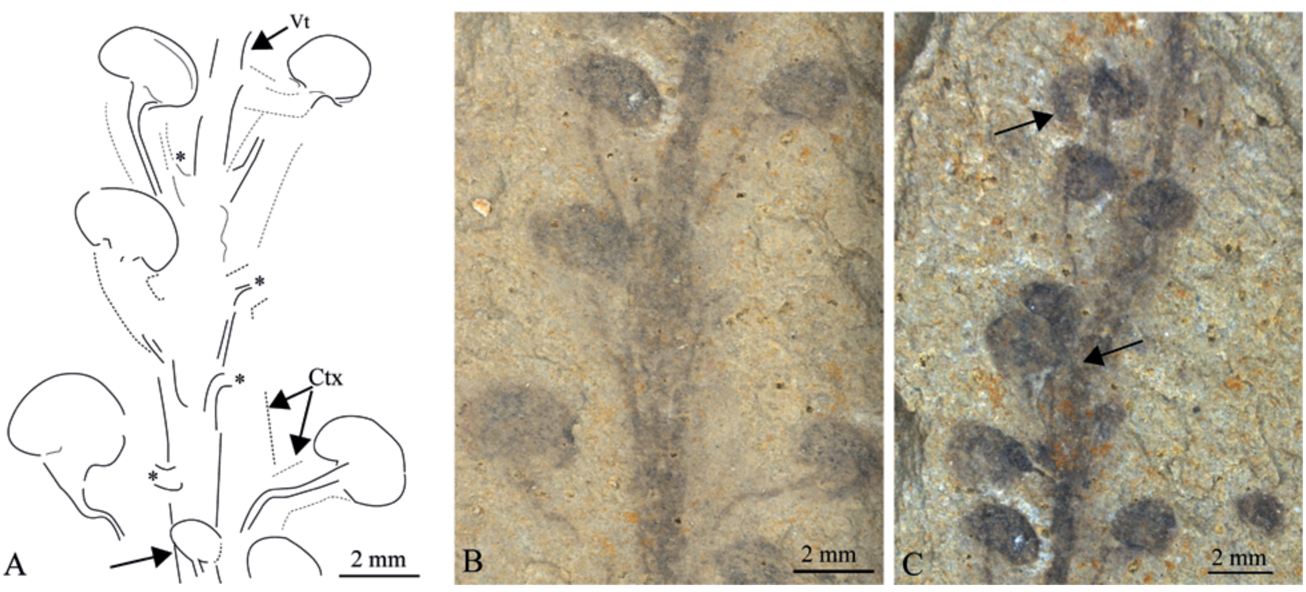

Figure 6. cf. *Zosterophyllum* sp. A. (part, NMV P256740.1): a, line drawing of medial region of the spike seen in B; b, the cortex (Ctx) is represented by a tincture of light grey in comparison to a darker coloured vascular trace (Vt). Some perturbations and depressions (*) likely represent additional stalks. Note small proximal sporangia (at arrow) in a central position on the fertile axis; c, distal part of spike – lower arrow at stalk that has been pushed across the fertile axis. At the upper arrow sporangium with no stalk, partially behind another sporangium. Smaller sporangia more centrally located suggests distal part of spike may be helically inserted. Images taken by Rodney Start © Museums Victoria.

helically arranged in some specimens of *Z. myretonianum* and attributed it to the compression of widely spaced spirally arranged sporangia, giving this misleading appearance (Edwards, 1975: 261). Furthermore, Gerrienne (1988: 328) made similar observations, adding that the difference may also be due to different ontogenetic stages of individual spikes, and Gensel (1982) noted for *Z. divaricatum*, sporangia bending and twisting of sporangia to one side.

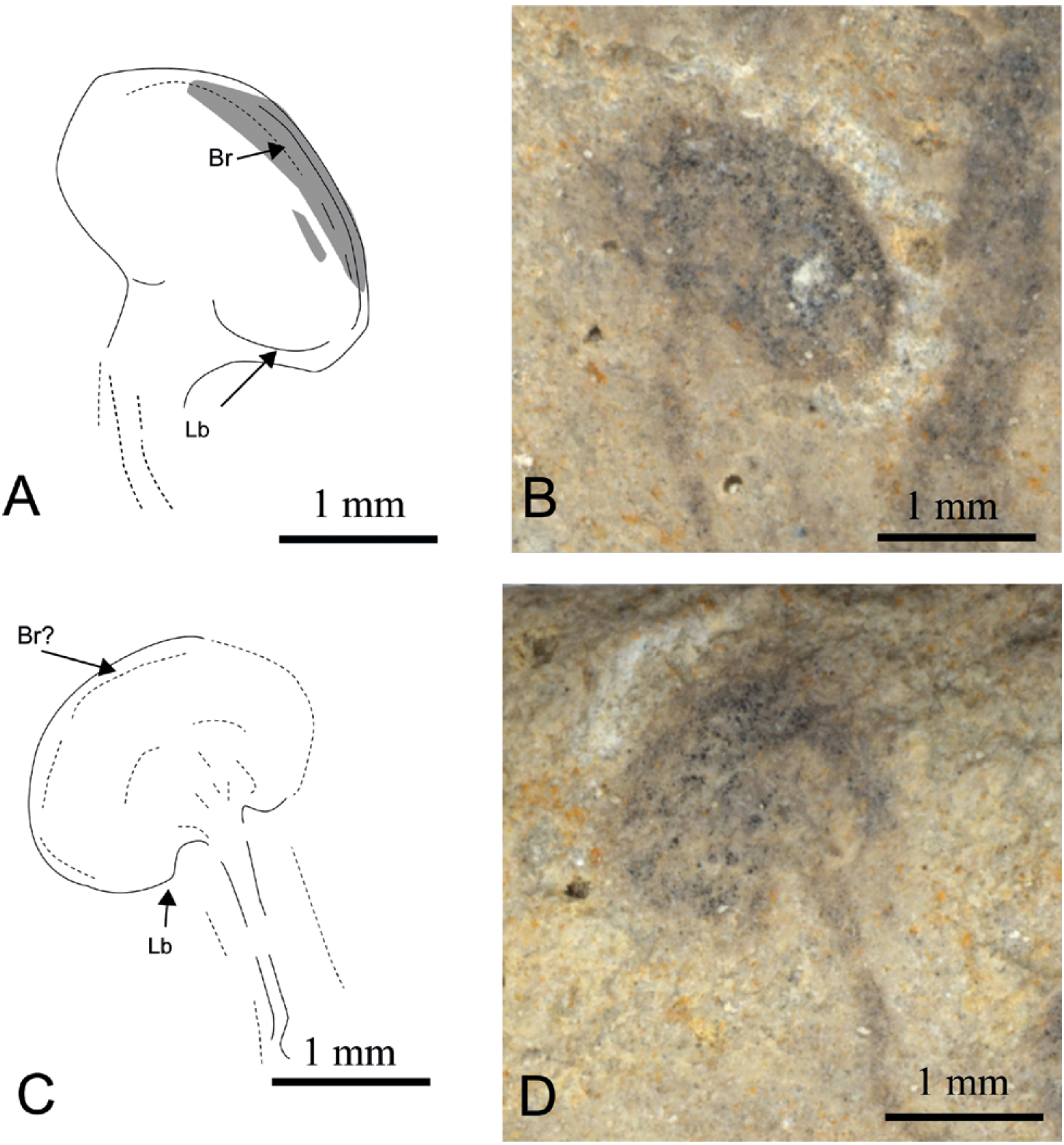

Figure 7. cf. *Zosterophyllum* sp. A. (part, NMV P256740.1). Interpretative line drawings: a, c, sporangia in b, d, respectively. The sporangia have weakly developed lobes (Lb), and a lack of a clear junction between the stalk and sporangium. A fine border (Br) is visible only alone distal margins.

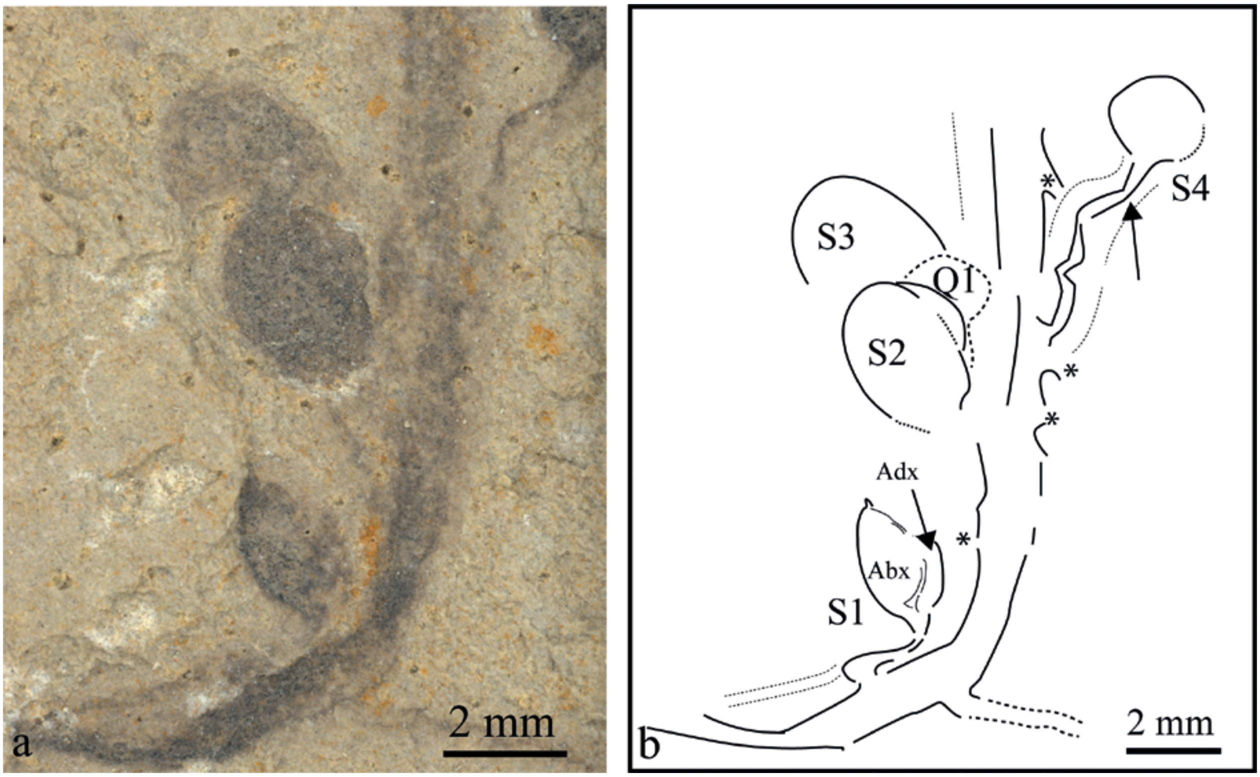

Figure 8. cf. *Zosterophyllum* sp. A. (part, NMV P256740.1): a, proximal region of spike; b, interpretative line drawing. Sporangia one and two (S1–2) appear infolded, with both abaxial (Abx) and partial adaxial (Adx) valves visible in sporangia and two perturbations and depressions (*) possibly representative of additional stalks that were not preserved. Q1, shadowing of possible sporangium, and upper arrow shows change in orientation of stalk beneath sporangium four.

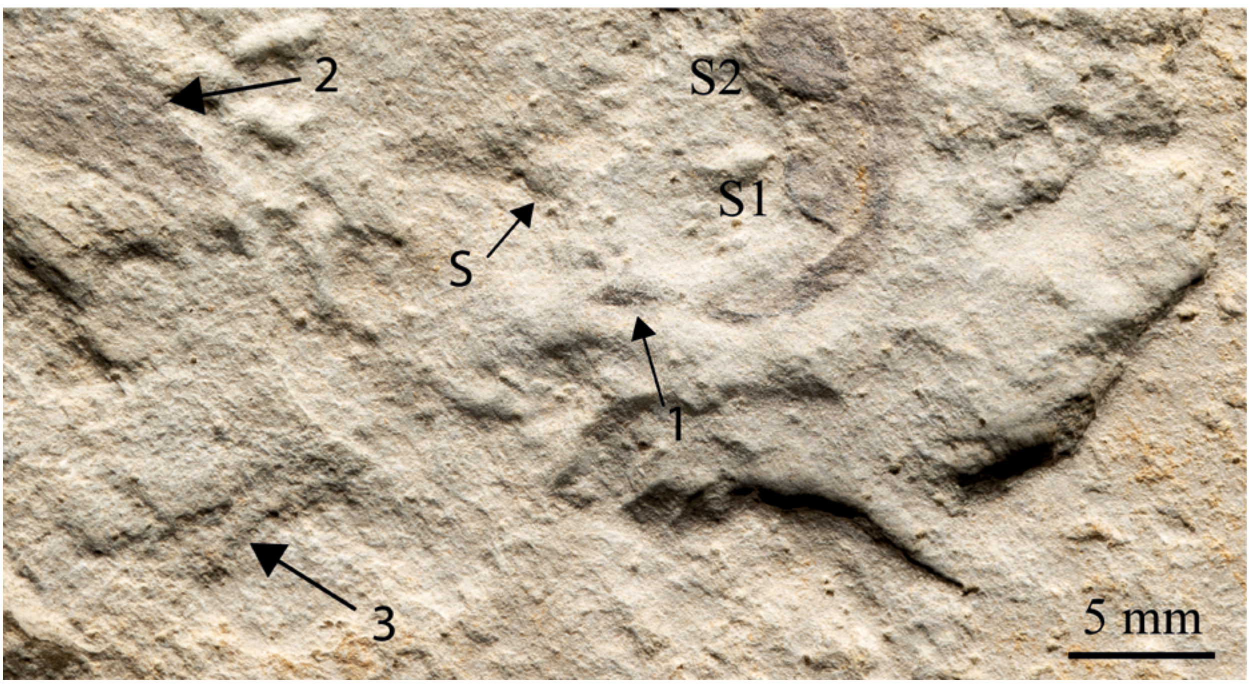

Figure 9. cf. *Zosterophyllum* sp. A. (part, NMV P256740.1). Proximal region of spike with sporangia one (S1) and two (S2) visible and fertile axis curving into ?rhizomatous region (arrow 1) and possibly extending out towards axes (arrows 2 and 3). Isolated sporangium (S) in same orientation as sporangia in spike. Image taken by Rodney Start © Museums Victoria.

In comparison with species within the subgenus *Zosterophyllum* with reniform sporangia, the specimen is closest to *Z. bifurcatum* Li and Cai, 1977; *Z. deciduum*; *Z. myretonianum* Lang, 1927; *Z. ramosum*; *Z. rhenanum*; *Z. yunnanicum* Hsü, 1966; and *Z. shengfengense*, all of which have sporangia in approximately the same size range.

Zosterophyllum myretonianum is one of the best studied *Zosterophyllum* to date (Edwards, 1975; Lang, 1927; Lele and Walton, 1961). Edwards (1969: 261) noted when examining *Z. myretonianum* from Aberlemno, Scotland, that they possessed spikes with different levels of sporangial packing, such that the specimens could be divided into compact, intermediate and laxly arranged spikes. The sporangial–stalk interface of *Z. myretonianum*, according to Edwards (1975), possesses a dome-like region at the point of insertion on the sporangium of some of the specimens, which produces its reniform shape. It is noticeable that in *Z. myretonianum*, despite different stages in development, the orientation of the sporangial stalk remains largely constant, with the sporangial stalk inserted at almost 90° (Edwards, 1975) to the fertile axis before curving upwards immediately with the sporangium held erect. This clearly differs from the specimen where the sporangial stalks extend from the fertile axis, curving upwards only just beneath the sporangium and in some cases attached to the sporangium at an angle, thus producing a splayed appearance. *Zosterophyllum bifurcatum* possess well-developed lobes and much narrower stalks than the specimen reaching up to 0.6 mm wide according to Li and Cai (1977) and Hao and Xue (2013). *Zosterophyllum rhenanum* also possess well-developed sporangial lobes and has a noticeable junction between sporangium and stalk, and a large border of 0.6 mm (Hao and Xue, 2013; Schweitzer, 1979). *Zosterophyllum deciduum* has weakly developed sporangial lobes (Gerrienne, 1988: 322), similar to the specimen, but the sporangial stalks were wide (0.4–0.75 mm) near the fertile axis and narrow (0.1–0.3 mm) near the sporangium (Gerrienne, 1988: 320), with the contact between the sporangium and subtending stalk producing a clear junction with no evidence of widening beneath the sporangia (Gerrienne, 1988: 331). These characteristics are at odds with what is observed with the specimen where sporangial stalks remain parallel in width before widening into the base of the sporangium. Furthermore, *Z. deciduum* bifurcates both below and within its fertile parts (Gerrienne, 1988).

In comparison with *Zosterophyllum* from the South China plate with similar sporangial dimension, *Zosterophyllum shengfengense* from the Lochkovian, Lower Devonian of Xitun Formation, Yunnan, China, differs from the specimen in not possessing any sporangial basal lobes, and shorter stalks, 0.5–0.8 mm wide and 0.8–1.6 mm long (Hao et al., 2010; Hao and Xue, 2013). Furthermore, *Zosterophyllum shengfengense* (Hao et al., 2010: 222), like *Z. myretonianum* (Lele and Walton, 1961: 471), possess tubercles proximally on the plant, unlike the specimen (Hao et al., 2010: fig. 2a). *Zosterophyllum yunnanicum* from the Xujiachong Formation, Yunnan, possess crowded spikes with up to 50 sporangia circular to elliptical in face view, dehiscence zone up to 0.5 mm wide, stalks 0.3–0.9 mm wide and 0.6–3.0 mm long inserted an acute angle to the fertile axis and widening into the bases of sporangia (Edwards et al., 2015: 223). The stalks emanate perpendicular to the spike, based on Edwards et al. (2015: pl. 4, figs 1, 2) and immediately reorientate producing 30°–40° to the fertile axis (Wang, 2007: 528). This reorientation of the stalks near the fertile axis differs significantly from the specimen, where the stalks reorientate only just beneath each sporangium. Furthermore, *Z. yunnanicum* produces a dome-like structure at the stalk–sporangium interface (Edwards et al., 2015).

Comparison with known Victorian zosterophyll taxa. Only four zosterophylls have thus far been described from Victoria. These include *Z. australianum* Lang and Cookson, 1930; *Z. ramosum* Hao and Wang, 2000; *Parazosterophyllum timsiae* McSweeney et al., 2020; and *Gippslandites minutus* McSweeney et al., 2020. Both *Z. australianum* and *Z. ramosum* occur in the Norton Gully Sandstone Formation of Victoria and are younger than the specimen, which is currently only known from the underlying Wilson Creek Shale. *Zosterophyllum australianum* occurs at North Road Quarry, Walhalla, Victoria, and Yunnan (Posongchong Formation), China (Hao and Xue 2013; Lang and Cookson 1930). *Zosterophyllum australianum* possess sporangia that are noticeably larger than the specimen and are longitudinally elliptical or fan-shaped, 2.8–8.0 mm wide and 2.2–5.0 mm high, with short stalks inserted on the fertile axis at 90° (Hao and Xue, 2013; Lang and Cookson, 1930). *Zosterophyllum ramosum* occur at Mount Pleasant and Halls Flat Road, Alexandra (Cookson, 1935; Hao and Wang, 2000). Mount Pleasant Road is the type locality of *Yarravia* (*Hedeia*) *corymbosa* Cookson, 1935, and cf. *Baragwanathia longifolia*, cf. *Yarravia oblonga*, cf. *Hostinella* and *Pachytheca* sp. have been found by Cookson (1935) to occur with *Z. ramosum* (McSweeney et al., 2021a, b). *Zosterophyllum ramosum* was originally called *Z. australianum* by Cookson (1935: pl. 10, figs 9–12), but was later reinterpreted by Hao and Wang (2000: 31) to be a new species *Z. ramosum*, which also occurs in Yunnan (Posongchong Formation), China. *Zosterophyllum ramosum* possess circular to reniform sporangia similar to the specimen, but the sporangia are larger, being 1.6–6.0 mm wide and 1.9–5.5 mm high, on stalks up to 5.0 mm inserted on the fertile axis at 15°–35° (Hao and Wang, 2000; Hao and Xue, 2013). Both *Z. ramosum* and *Z. australianum*, according to Hao and Xue (2013: fig. 6.5), possess apple-shaped Za-type sporangium with extended thickened margins, a character not found in the specimen. *Parazosterophyllum timsiae* is from Ghin Ghin Road, Yea, in the base of the Humevale Formation and based on Rickards & Garratt (1990) Pridoli, upper Silurian–Pragian, Lower Devonian, and may be either coeval or older than the specimen and differ significantly from the specimen with its spike terminating lateral branch (McSweeney et al., 2020). *Gippslandites minutus* is from an outcrop of the Boola formation (Lochkovian–Pragian, L. Devonian) near Boola Quarry, Tyers, Victoria (Tims, 1980; McSweeney et al., 2000). The Boola formation is slightly older than the Wilson Creek Shale, which overlies the Boola formation at Coopers Creek according to Edwards et al. (1997: 39). *Gippslandites minutus* differs from the specimen because its sporangia are much smaller, 0.6–2.6

mm wide and 0.3–1.9 mm high, and differ significantly from *Zosterophyllum* spp. with anisovalvate sporangia (McSweeney et al., 2020).

The defining characteristic of the specimen is primarily the angle of insertion of the vascularised stalks and no overlap between vertical adjacent sporangia. As noted by Edwards (1975: 264), the most useful characters in species delimitation within *Zosterophyllum* are stalk and sporangial characters. It is clear that the specimen differs from zosterophylls from Victoria primarily on sporangial morphology and symmetry. As the sporangial stalks were likely longer in life when turgid and prior to degradation resulting in convoluted vascular trace, the lack of vertical overlap of sporangia and vascularisation of the stalks, and clear demarcation of insertion points on the fertile axis means the specimen cannot be readily put into the subgenus *Platyzosterophyllum*, and is thus assigned to cf. *Zosterophyllum* sp. A. until better material becomes available to allow for further assessment of its phylogenetic and taxonomic position.

cf. *Zosterophyllum* sp. B.

Gen. et sp. indet.

Figures 10, 11

Material. NMV P256742.1 and P256742.2 (P4-5 field note identifier), part and counterpart, respectively.

Locality. P4 is equivalent to Loc. 1 in Garratt (1978: fig. 2), and occurs on Ghin Ghin Road, 8 km northwest of Yea township, central Victoria.

Horizon and age. Humevale Siltstone, Pragian–Emsian, Lower Devonian (Edwards et al., 1997; Garratt, 1978; Rickards, 2000; Rickards and Garratt, 1990; VandenBerg et al. 2000; VandenBerg pers. comm. June 2021).

Description. Single specimen, comprising compact spike, with part and counterpart preserved in semi-relief as an iron oxide coated impression and cast, only gross morphological features are visible (fig. 10). The spike measures 21 mm high and 10 mm

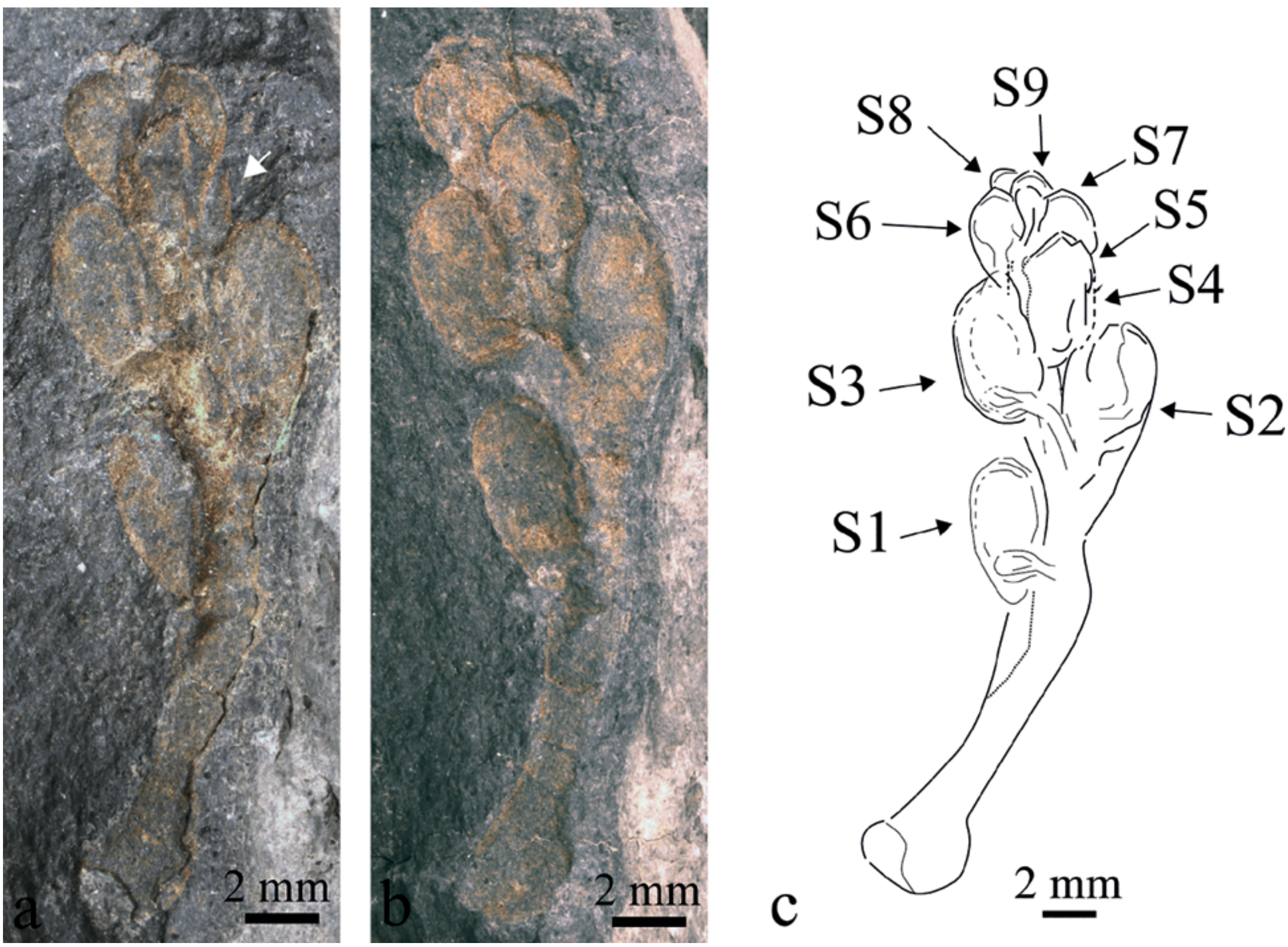

Figure 10. cf. *Zosterophyllum* sp. B, from the Humevale Siltstone, Ghin Ghin Road, Yea: a, part (NMV P NMV P256742.1); b, counterpart (NMV P NMV P256742.2) respectively; c, line drawing, with S1–9 (sporangia one to nine). Note: Part image reversed to be in the same orientation as the counterpart. Note. Arrow in part, points to sporangium 4, which is obscured in the counterpart.

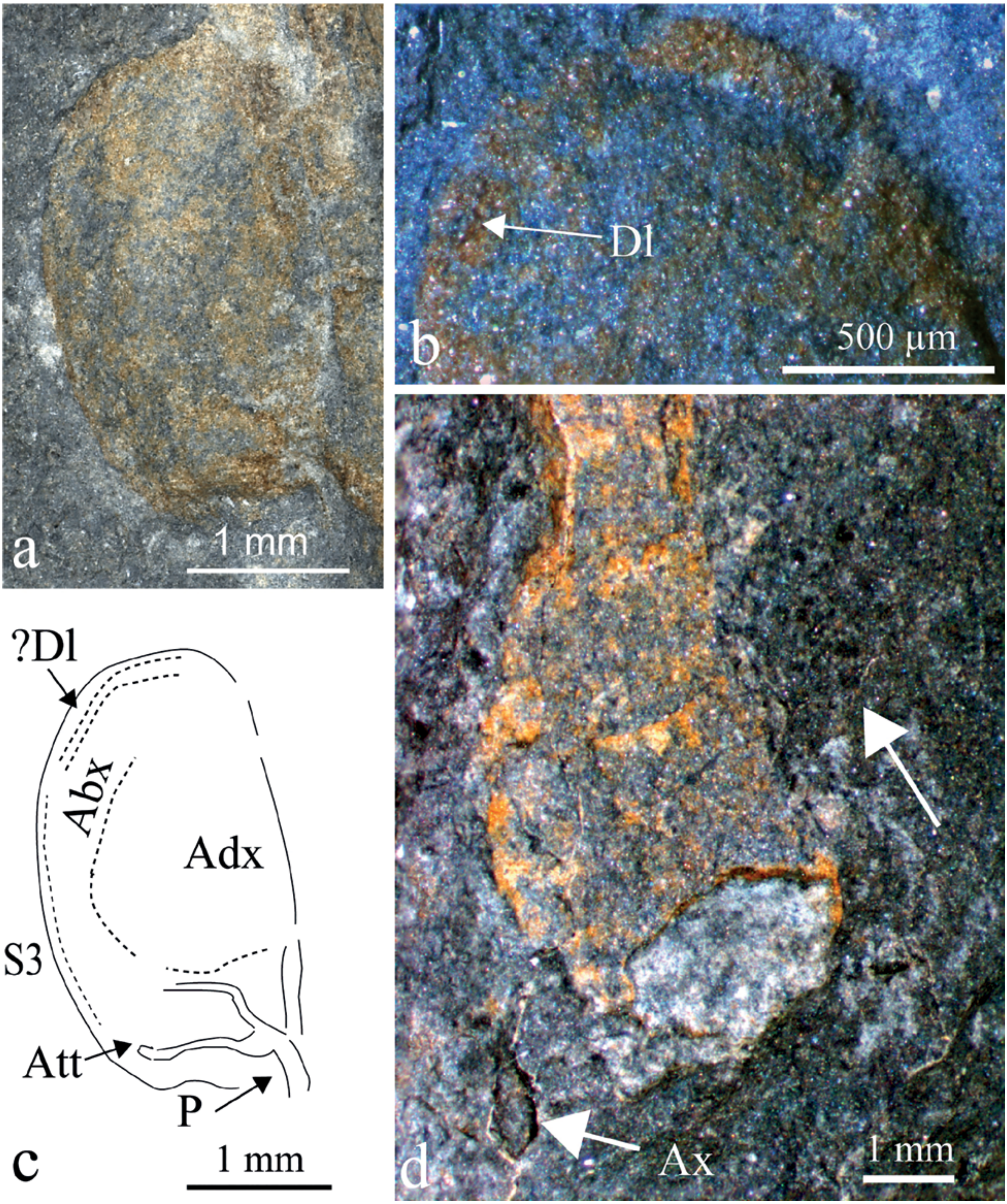

Figure 11. cf. *Zosterophyllum* sp. B. NMV P256742.1: a, c, (line drawing) sporangium 3 (counterpart) in-folded, with stalk attachment widening out in basal region of sporangium. Poorly defined dehiscence zone (zone) and line; b, sporangium one (counterpart) with border visible; d, basal oval structure (part), with what appears to be a much smaller spike emanating from it (at arrow), and a poorly preserved axis beneath the oval structure.

wide, with at least nine sporangia arranged helically, becoming more compact distally. The fertile naked axis measures 1.5–3.75 mm wide, narrowing distally before terminating in sporangium nine. Sporangia in face view (1.2–3.0 mm wide and 3.9–4.3 mm long) occur in the distal part of the spike and are circular to oblong. Proximally, sporangia one to three are in lateral view, being longitudinally elliptical and infolded. Sporangia are inserted at an angle of ~20°. Proximally on the spike there is an elliptical (lateral view) junction at the point of attachment (face view) on the abaxial valve between the stalk and the sporangium. The stalks are decurrent, narrowing slightly before widening distally at the base of the sporangium. The sporangia possess a dehiscence zone along their entire distal margins, with a border 0.1–0.2 mm wide gradually tapering proximally towards the stalk attachment.

Remarks. There is a notable disparity in size between the much larger proximal sporangia (S1–5) and distal sporangia (S6–9), suggesting the spike may be immature. Sporangia one–three are in a lateral position and are infolded, a common feature seen especially in laterally placed sporangia of *Zosterophyllum*. It suggests that the sporangia may have originally had relatively flat bodies, as proposed by Lang (1927) when explaining this feature in *Zosterophyllum myretonianum*. The points of attachment of the stalk to the sporangia are visible on sporangia one and three (Figs 11a, c), with the stalks widening into the base of the sporangia. The attachment is elliptical, and it is possible that the raised regions defining the elliptical region, which appear partially raised, may reflect the splitting of the attachment at the base of the sporangium, possibly feeding each of the valve. However, the preservation is too poor and this remains equivocal. The attachment occurs on the adaxial side of the valve, but the demarcations between both valves are faint or absent on the sporangia. Most of the distal sporangia show the stalk centred beneath the sporangium, with a gradual widening of the stalk into the valve. Sporangium seven, which is in face-view, appears to show the widening of the distal part of the stalk on the lower part of a valve, producing a sub-circular zone of attachment. Sporangium five, while poorly preserved, is in side view and greatly compressed laterally with the projecting edge of the border visible in the apex, and a fine stalk is present in the basal region. The adaxial valve only appears marginally darker than the surrounding matrix and is convex, while the upper valve is flatter and delimited by its iron-oxide colouration. Sporangia four and six also appear to show a slight separation at the distal-most region of the valves. This may be a result of compression as the sporangia are small relative to the proximal sporangia, suggesting they were not fully mature.

The dehiscence line can be seen along the distal margins of the proximal sporangia, visible down to the stalk attachment (fig. 11c) but is only visible on some of the distal sporangia. There is a dehiscence zone beside the dehiscence line no wider than 0.2 mm and is clearest on the proximal sporangia.

The proximal part of the fertile axis expands into an oval-shaped body (fig. 11d) that measures 3.74 mm wide and 5.80 mm high. The point where the axis starts increasing in diameter was taken as the start of this structure because there is no other way to differentiate it from the axis. The oval body is similar to the corm-like structure found basally on *Horneophyton lignieri* Barghoorn and Darrah (= *Hornea lignieri* Kidston and Lang, 1920). However, because no anatomy is preserved, its nature remains equivocal and may be a quirk of preservation. A small, fine, faint linear structure (fig. 11d) appears to emanate from the oval body, but remains equivocal because sampling did not reveal any organic remains and high magnification did not reveal any morphological characters.

The specimen fits into the class Zosterophyllopsida based on the presence of naked axes, cauline sporangia made up of two valves that dehisce along their distal margins, and vascularized stalks (Croft and Lang, 1942). The Zosterophyllopsida includes two orders, Zosterophyllales and Gosslingiales, and because this specimen possessed a terminal sporangium, it has been assigned to order Zosterophyllales. Numerous characteristics are notably absent, such as H- or K-branching and circinate vernation. Because the sporangia were not in rows, the specimen was excluded from the subgenus *Platyzosterophyllum* and tentatively placed into the subgenus *Zosterophyllum*. However, it was difficult to determine the true morphological outline of the sporangia, with some of the distal sporangia appearing slightly longer than wider. Furthermore, the absence of sporangia proximally in face view added to the uncertainty of whether the sporangia were slightly vertically elongate. Distally, the sporangia are poorly preserved with no unequivocal demarcation of both the valves and junctions between the valves and their subtending stalks. For the subgenus *Zosterophyllum*, the sporangia are reinform, fan-shaped and isovalved, and are excluded if anisovalvate or vertically longer than wide according to Edwards et al. (2016) and Edwards and Li (2018a). Additionally, the presence of an oval region at the proximal end of the fertile axis added further doubt to its true assignation, and so the specimen was placed into cf. *Zosterophyllum* sp.

cf. *Zosterophyllum* sp. B differs from known *Zosterophyllum* spp. from Victoria (*Z. australianum* and *Z. ramosum*), despite the limited characters available for comparison. *Zosterophyllum australianum* possess horizontally elliptical sporangia with large, thickened margins (0.4–1.1 mm wide) and sporangia far larger than cf. *Zosterophyllum* sp. B., reaching up to 8.0 mm wide and 5.0 mm high (Hao and Xue, 2013; Lang and Cookson, 1930). Additionally, the stalks of *Z. australianum* are inserted at an angle of ~90°, in contrast to ~20°° in cf. *Zosterophyllum* sp. B. *Zosterophyllum ramosum*, like *Z. australianum*, possess much larger sporangia, reaching up to 6.0 mm wide and 5.5 mm high, and are circular to reinform in shape (Hao and Wang, 2000).

In comparison with other zosterophylls with vertically elongate sporangia outside the subgenus *Zosterophyllum*, cf. *Zosterophyllum* sp. B. appears distinct, despite the paucity of available characters with which to compare. For example, *Guangnania cuneata* Wang and Hao, 2002, possess anisovalvate upright sporangia, but differ from cf. *Zosterophyllum* sp. in the spike not being compact, the sporangia being much longer than wide (3.9–6.2 mm high and 1.5–1.9 mm wide) and not possessing a terminal sporangium. *Yunia dichotoma* Hao and Beck, 1991, from the Zhichang section of the Posongchong Formation, differs from cf. *Zosterophyllum* sp. B in the morphology of the sporangia, which are elongate–elliptical to ovoid, but the sporangia did not form spikes (Hao and Beck, 1991). Additionally, the axes of *Y. dichotoma* possess small spines (Hao and Beck, 1991). *Huia recurvata* Geng, 1985, of the Posongchong Formation, Yunnan, China, produced sporangia that were ovate to ovoid 2D to 3D (Hao and Xue, 2013: 70). *Huia recurvata* differs in having adaxially reflected closely arranged sporangia as opposed to the crowded arrangement seen in cf. *Zosterophyllum* sp. B., with sporangia 3–5 mm wide and 6–10 mm high (Hao and Xue, 2013).

Primarily, because the specimen lacks unequivocal evidence as to the characteristics of the sporangia, such as whether the sporangia are longer than wide, it has been placed in cf. *Zosterophyllum* sp. B.

Discussion

The term sporangial stalk is used with regards to cf. *Zosterophyllum* sp. A. for convenience, similar to Edwards (2006: 96), but it is possible they represent lateral branches with sessile sporangia, as proposed by Hueber (1992: 480) in his examination of zosterophyll sporangial and based on his hypothesis that some cooksonioids were the progenitor of this group. The presence of a vascular trace in the sporangial stalk of cf. *Zosterophyllum* sp. A. adds credence to Hueber's hypothesis (category 3) and has been observed with *Z. divaricatum* (Gensel, 1982: 654), *Z. myretonianum* (Edwards, 1975: 262; Lang, 1927: 450), and according to Niklas and Banks (1990: 278), *Z. rhenanum* and *Z. longhaushanense*. Niklas and Banks (1990: 277) proposed two patterns of fertile growth within zosterophylls governed by apical meristematic growth and speculated the difference in symmetry for *Z. myretonianum*, *Z. fertile* and *Z. llanoveranum* was due to uncanalised growth and that the nature of the apices (terminate and non-terminate) was the key to determining the type of meristematic growth. Interestingly Niklas and Banks (1990: 278), in discussing bilateral symmetry, postulated that the stalks were not the same as fertile axes and the lateral cluster of initials producing the stalks and sporangia would likely result in limited to no vascularisation of the stalk. This limited vascularisation of lateral axes appears to occur with cf. *Zosterophyllum* sp. A., whereby the apical initials of lateral axes were limited to just a single axis before terminating in a sporangium.

Both cf. *Zosterophyllum* sp. A. and cf. *Z. fertile* possess sporangia arranged in rows on their spikes, and this is the first time this arrangement has been described for Victorian Devonian flora. The zosterophyll assemblages from China, particularly those from the Pragian Posongchong Formation of the South China Plate, have predominantly been of sporangia inserted helically into the spike (Hao & Xue, 2013). Only three cases of sporangia occurring in rows in spikes have been recorded: *Zosterophyllum longhuashanense* Li and Cai, 1977; *Distichophytum* sp.; and *Amplectosporangium* (*Oricilla*) *unilaerale* Edwards and Li, 2018 (Edwards and Li, 2018; Hao and Xue, 2013). Another, *Ornicephalum (Zosterophyllum) sichuanense* Edwards and Li (2018: 100), superficially appears to show two-rowed sporangia. The geographical location of Victoria during the Pragian–Emsian, Lower Devonian, approximately 30° south of the equator, far from both the South China Plate and other known *Zosterophyllum* localities, suggests two of the specimens described herein may be new taxa. The palaeocontinental positioning of Victoria and the South China Plate during the Lower Devonian is based on the work of Mitchell et al. (2012) and Torsvik and Cocks (2019), and is summarised in McSweeney et al. (2020). Australia and South China have only two species in common thus far – *Z. australianum* and *Z. ramosum* – and the specimens described herein further add to the hypothesis of limited floristic exchange, as espoused by Xue et al. (2018: 98).

Conclusion

This study has confirmed the first occurrence of bilateral symmetry in Victoria. Despite the dearth of fossil evidence, three additional forms – cf. *Zosterophyllum* sp. A, cf. *Z.* sp. B. and cf. *Z. fertile* – indicate greater diversity in the region during the Silurio–Devonian than previously known. However, forms with better preservation are required to determine their taxonomic positions with certainty.

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Disclosure Statement

No potential conflict of interest was reported by the authors.

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