

RHYNIOPHYTINA AND TRIMEROPHYTINA FROM THE EARLY LAND FLORA OF VICTORIA, AUSTRALIA

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ABSTRACT. New records of northern hemisphere plant genera are described from the Lower Plant Assemblage (Late Silurian, Ludlovian) and the Wilson Creek Shale (Early Devonian, Pragian/Siegenian) of Victoria, Australia. The genera, the rhyniophyte *Salopella* of which there are two new species *S. australis* and *S. caespitosa*, and *Dawsonites*, represented by *D. subarcuatus* sp. nov., which is the first recording of a trimerophyte in Victoria and probably in the Southern Hemisphere, were found associated with *Baragwanathia* and are new additions to the *Baragwanathia* flora.

SINCE the work of Lang and Cookson (1930, 1935) and Cookson (1935, 1949) no formal studies have been made on the *Baragwanathia* flora of the Lower Devonian of Victoria, Australia. For many years this flora was regarded as Silurian, the oldest vascular land plant flora in the world. Elles (in Lang and Cookson 1935) had identified the associated graptolite as *Monograptus uncinatus* Tullberg (an Early Ludlow species), which often occurred on the same bedding plane as specimens of *B. longifolia* Lang and Cookson. Investigations by Jaeger commencing in 1959 (see Jaeger 1966) led to the description of this as a new species, *M. thomasi* Jaeger. Associated with *M. thomasi* and slightly higher is *M. aequabilis notoaequabilis* Jaeger and Stein. The range of this latter species in other parts of the world is Pragian. *M. thomasi* has since been identified from Malaya (Jaeger 1970) and as *M. aff. thomasi* in Russia (Koren' 1971) in rocks believed to be Pragian. Jaeger considers that the evidence suggests the *Baragwanathia* flora as described by Lang and Cookson (1930, 1935) is Pragian, a view with which Koren' concurs. However, the precise age range of *M. thomasi* is still uncertain. The range of *Baragwanathia* itself extends above that of *M. aequabilis notoaequabilis* and, in Victoria, below that of *M. thomasi*.

Garratt (1978) reported two distinct *Baragwanathia* floras from the Yea district: the Upper and Lower Plant Assemblages. The Upper Plant Assemblage is equivalent in age to the flora described by Lang and Cookson. The 1929 collecting party (Harris and Thomas 1941) obtained plant fossil material from the Upper and Lower Plant Assemblages in the Yea district. The Lower Plant Assemblage material was collected from a road cutting about 30 m from the Limestone Road locality described here. None of this material had been included in Lang and Cookson's papers on the *Baragwanathia* flora. The Upper Plant Assemblage material illustrated by Lang and Cookson (1935) was collected from Killingworth Road, Yea.

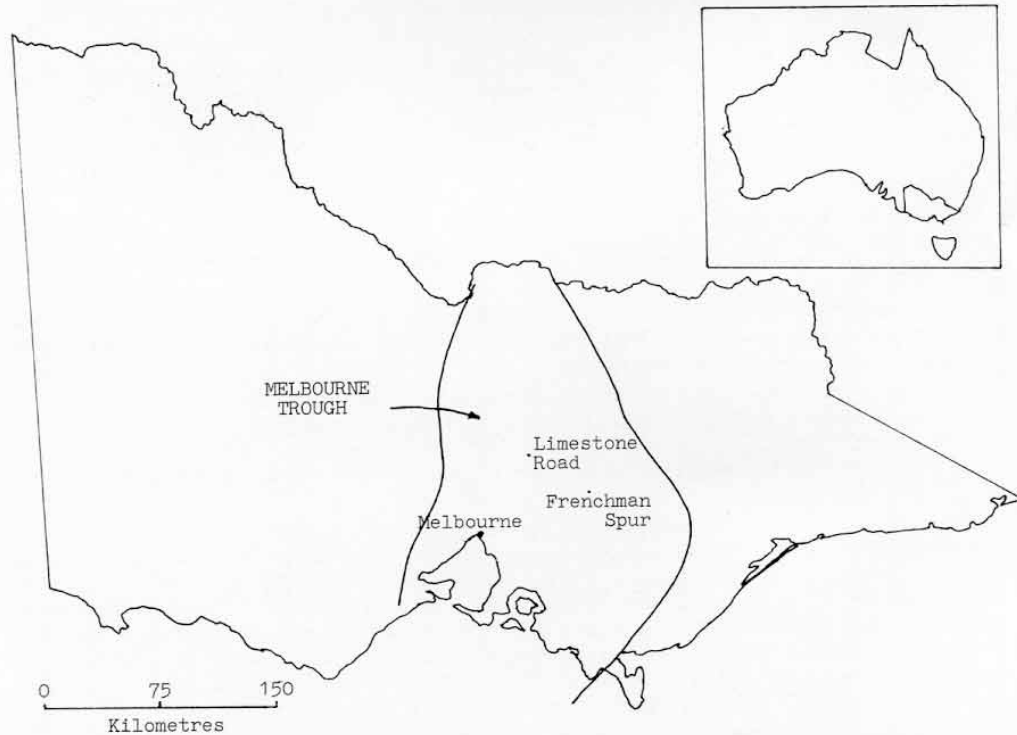
Separating the two assemblages is 1,700 m of virtually unfossiliferous sandstone. The Lower Plant Assemblage contains the oldest known *Baragwanathia* and is regarded, somewhat controversially, as being of Ludlovian age (Edwards *et al.* 1979; Garratt 1981). The dating, based initially on field evidence, is now on the basis of associated graptolites (Rickards 1982, pers. comm.). While no new species have been added to the *Baragwanathia* flora in the intervening years since the 1930s, when the late Dr. Isabel Cookson did her pioneering work, it is clear from the new records reported here, together with others still under investigation, that the *Baragwanathia* floras are more diverse than have been recognized.

LOCALITIES AND MATERIALS

LOCALITY 1. Frenchman Spur: roadside exposure on the fire access track known as Frenchman Spur Road about 10 km west of Matlock (Grid reference 077-656. Matlock: Australia Sheet 8122—IV, 1:50,000) (text-fig. 1).

The exposed strata are near the top of the 150 m thick Wilson Creek Shale which outcrops in the area at a number of localities that have yielded *Baragwanathia*. The unit comprises a fossiliferous shale interbedded with thick siltstones. Sediments at Frenchman Spur when fresh are hard and grey-black; they are almost impossible to split along bedding planes. The weathered material, which is buff coloured, splits easily and was the source of most of the specimens. Preservation of the plant fossils varies from compressions with considerable amounts of fragmentary mineral to pink-stained impressions. The Wilson Creek Shale has been subjected to at least one generation of folding which appears to have fragmented the mineral remains of the plant into microscopically small pieces, often arranged in two diagonal rows with the space in between filled with secondary silica. Most of the plant detail and cellular structure has been lost. Maceration with Schulze's solution yielded no fragments or spores; cellulose acetate film pulls failed to show any structure or *in situ* spores in either fresh or weathered rock.

Age and correlation. Early Pragian (= Siegenian); *M. thomasi* is sometimes found on the same bedding plane as plants, but more frequently in dense clusters on different planes. *M. aequabilis notaequabilis* is not present, but has been recorded at nearby localities in the Wilson Creek Shale.



TEXT-FIG. 1. Locality map showing location of the Melbourne Trough and the two collection sites.

The only other animal fossils are eurypterid fragments. The flora, therefore, is at the same stratigraphic level as the Upper Plant Graptolite Horizon (Couper 1965; Garratt 1978; Jaeger 1966) and is of Early Devonian age.

Flora. Rhyniophytina: *Salopella australis* sp. nov., *S. caespitosa* sp. nov., *Yarravia oblonga* Lang and Cookson, *Hedeia* spp. Zosterophyllophytina: *Zosterophyllum* sp., other undescribed zosterophylls. Lycophytina: *B. longifolia* Lang and Cookson, *B. sp.*, other lycopods, fragmentary but not *Baragwanathia*. Trimerophytina: *Dawsonites subarcuatus* sp. nov.

The site has been mentioned as a *Pachythea* locality (Moore 1965) but this identification has not been substantiated.

LOCALITY 2. Limestone Road, Yea: a recently widened road cutting 2 km south-east of Yea. (Grid reference 466-088. Yea: Australia Sheet 7923—I, 1:50,000.) This locality was cited by Harris and Thomas (1941) as Brackley's Cutting, Geological Survey locality 4, by Couper (1965) as locality 62, and by Garratt (1978) as locality 4 (text-fig. 1).

The plant-bearing strata are thin brown to grey claystones near the top of the Yea Formation (see stratigraphic section in Garratt 1978), and occur immediately below the Rice Hill Sandstone member. The horizon is some 1,700 m stratigraphically below that of the main *Baragwanathia* floras (Upper Plant Graptolite Horizon). Preservation is very poor; often only a depression in the plane of the rock to indicate the outline (e.g. Pl. 32, fig. 5). Some remains are of a white mineral and others of a brown deposit, occasionally occurring together (Pl. 32, fig. 6). No cellular structure or spores have been found.

Age and correlation. Ludlow Series; Garratt (1978, 1981) considers the assemblage to be of Late Silurian (Ludlow) age. He bases this on detailed geological mapping in this region, together with evidence from the associated fauna and lithological affinities and especially on the presence of several graptolite species known only from Ludlow strata elsewhere. These are *Pristiograptus dubius* and *Bohemograptus* sp. *M. aff. uncinatus uncinatus* has not been recorded at Yea, but occurs together with these two species and *Baragwanathia*, some 3 km to the north (Garratt 1978, locality 1). The Limestone Road assemblage also contains undescribed gastropods, orthocerids, *Hyolithes* spp., *Necklania* (bivalve), and *Maoristrophia banksi* (brachiopod).

The relatively large size of the axes, up to 400 mm, suggests either that they have not been transported far or had been transported gently. Garratt (pers. comm.) believes that the plants came from the south.

Flora. Rhyniophytina: *Salopella australis* sp. nov., *Hedeia* sp. Zosterophyllophytina: At least one zosterophyll (report in preparation), two other probable zosterophylls. Lycophytina: *Baragwanathia longifolia*, at least one other lycophyte.

SYSTEMATIC PALAEOLOGY

Three new species have been erected. All material (except that on Pl. 32, figs. 5, 6) housed at the National Museum of Victoria.

Subdivision RHYNIOPHYTINA Banks 1968
Family RHYNIACEAE Kidston and Lang 1920
Genus SALOPELLA Edwards and Richardson 1974

Type species. *S. allenii*.

Salopella australis sp. nov.

Plate 32, figs. 1-6; Plate 34, figs. 4, 5; text-fig. 2A-C

Diagnosis. Axes with at least two dichotomies, 0.9-2.4 mm wide with central line. Plant at least 145 mm high. No obvious branching at the base of the sporangia. Sporangia 6.5-14.0 mm long and

1.3–2.0 mm wide, with parallel sides in the lower two-thirds of the presumed fertile portion. Sterile sporangial apex tapering to a point in the upper third. Spore characters unknown.

Range. Late Silurian (Ludlovian)–Early Devonian (Pragian).

Type locality. Frenchman Spur.

Horizon. Wilson Creek Shale (Pragian).

Holotype. NMV part and counterpart, P50,008. Plate 32, figs. 1, 2.

Derivation of specific name. 'australis'—southern.

Description. More than twenty specimens have been collected from two sites, Limestone Road (Ludlovian) and Frenchman Spur (Pragian). Most are compressions (*sensu* Schopf 1975) but some are so weathered that they have been reduced to impressions. Preservation varies from a pink stain on a buff-coloured matrix to a finely divided material of coaly appearance, as seen in specimens from Frenchman Spur, and red-brown and white minerals on similar coloured background from Limestone Road. One Limestone Road specimen (Pl. 32, fig. 3) is white on a blue-grey matrix, with its ultimate branches on different planes in the rock. The majority of specimens have had some covering matrix removed.

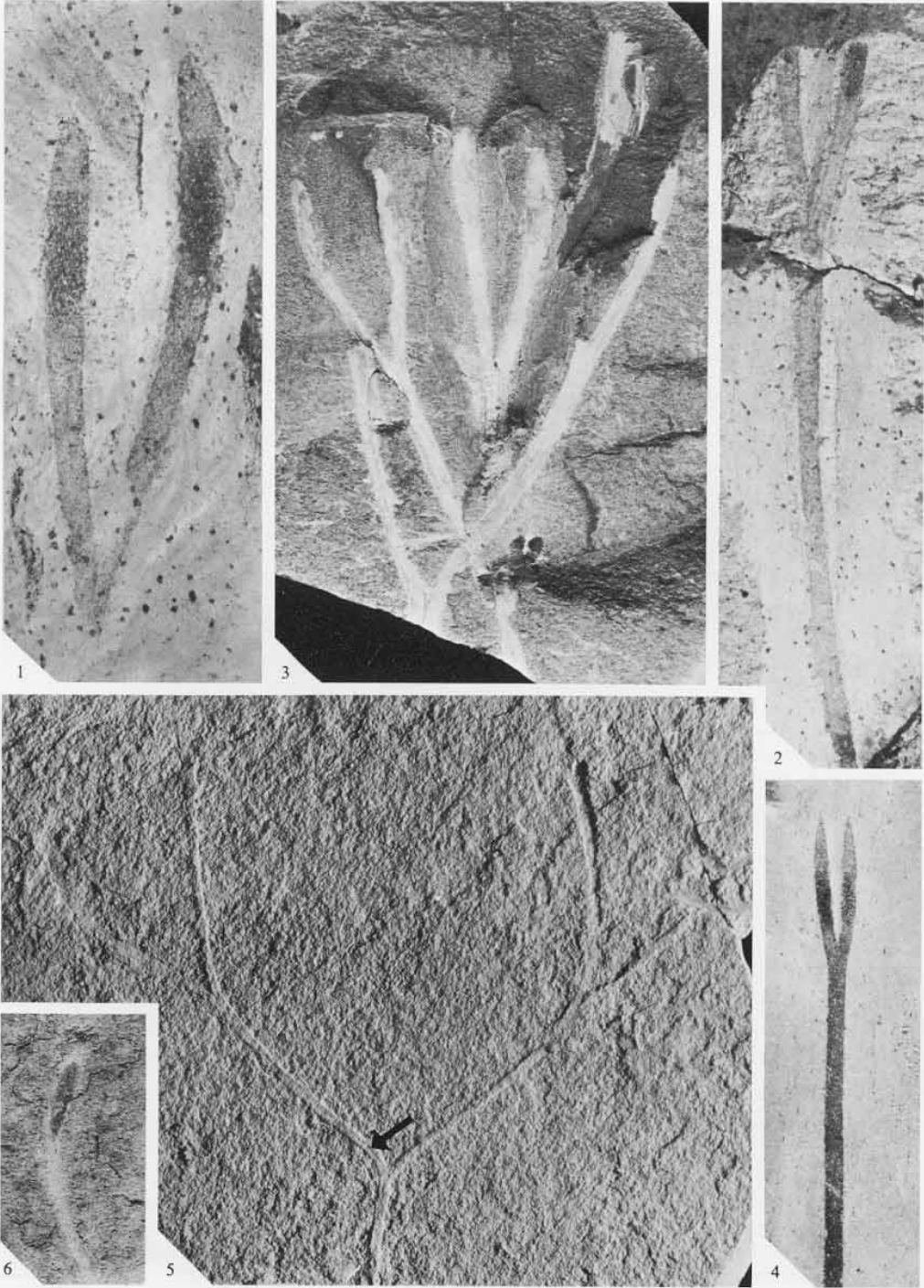
The specimens show the remains of a possible vascular trace, 0.22 mm wide, in some cases as a faint dark line in the centre of the stem (Pl. 32, fig. 1) and in others, a central ridge (Pl. 32, fig. 3). The ridge branches with the axis.

The maximum total length of axes is 145 mm. Eleven of the specimens are dichotomously branched (another possibly so) and of these, four have two dichotomies. Of the remaining six specimens, one is an isolated axis apex and the others are of axis lengths up to 40 mm. Axis width decreases with successive branching but remains constant between nodes. Maximum width is 2.4 mm and the minimum 0.9 mm. Average widths for the lowest branch are 2.1 mm (range 1.8–2.4 mm), the intermediate 1.8 mm (1.0–2.2 mm) and the ultimate branch 1.4 (0.9–1.7 mm).

Each axis terminates in a single presumed sporangium. In the better-preserved specimens an oval-shaped area of dark mineral is present a few millimetres below the apex. These areas are presumed to be sporogenous, although no spores could be isolated from them. The junction between axis and sporangium could not be clearly defined, as many axes show an increase in diameter 2–3 mm below the presumed spore mass. Measurement of the sporangia was taken from the base of the dark area or the remaining outline. Where there was no increase in the axis diameter below the sporangium the sporangial width was the same as that of its axis. Average length of twenty-six sporangia is 10.2 mm (range 6.5–14.0 mm). The average width of the sporangia is 1.8 mm (1.3–2.9 mm). The presumed spore-containing area where visible averaged 5.7 mm in length (4.4–7.5 mm). The sporangia are of acute convex shape in the presumed sterile upper portion. In half the specimens there is evidence of a slight indentation where the sterile tips connect with the fertile area (e.g. Pl. 32, fig. 5). The maximum widths of the sporangia coincide with those of the presumed fertile areas. The sporangia are parallel-sided for at least half their length.

EXPLANATION OF PLATE 32

Figs. 1–6. *Salopella australis* sp. nov. 1, 2, NMV P50,008 part and counterpart; holotype showing the sterile apex of the sporangium, the dark presumed sporogenous region and dichotomous branching; Frenchman Spur; fig. 1, $\times 3.8$, fig. 2, $\times 2.2$. 3, NMV P50,011; plant remains preserved as a white mineral on a steel-blue coloured matrix; the two branches with eight sporangia are most likely from the one plant (see reconstruction, text-fig. 2c); central ridge on the lower part of the plant is the probable remains of the vascular trace; Limestone Road, $\times 1.8$. 4, NMV P50,014; an axis with a dichotomy just below the sporangia; this specimen has the longest sporangia and is unusual in branching just below the dark spore masses; Frenchman Spur, $\times 1.1$. 5, one of the longest specimens (123 mm) from Limestone Road; although it cannot be seen from this illustration using a unilateral light source, the two sporangia on the left both have a dark area, the remains of a presumed spore mass; remains of the vascular trace are visible in the lower part of the axis (arrow); $\times 1$ (this specimen is from Dr. J. Douglas's private collection). 6, the extreme left-hand sporangium of fig. 5, showing the large dark presumed spore mass; photograph was taken using overhead light and high contrast film and paper; remainder of the specimen is not visible using this technique; $\times 1.5$.



TIMS and CHAMBERS, *Salopella*

Angles of the ultimate branches average 38° ($25\text{--}60^\circ$), while the lower branching angle is wider at 60° ($48\text{--}70^\circ$). The specimen illustrated on Plate 32, fig. 5 and text-fig. 2B has at first glance a much broader angle. If the angle is examined 1 mm from the dichotomy, it can be seen that the angle is 70° and the further spreading of the branches may be an artefact of deposition. In most examples, the branch axes curve in together until they become almost parallel.

As may be seen in Plate 32, fig. 1, naked axes of similar widths often occur on the same bedding planes as the specimens referred to as *Salopella*. Some of these naked axes are up to 200 mm long and often curved. There is little direct evidence of the habit of *Salopella*, but if the long axes are portions of this species, it is possible that the plant was partially prostrate. It is unlikely that such slender axes would exceed this height, although this would depend to some extent on stem anatomy.

In conclusion, the Victorian specimens are part of a small, open-branched plant, at least 145 mm high with slender naked axes terminating in elongate sporangia. Axes dichotomize at least twice, with successive planes of dichotomy, probably at 90° . The specimen illustrated in Plate 32, fig. 3 and text-fig. 2C demonstrates this and has different orders of branches on different planes in the rock. No spores could be isolated from the sporangia and no cell detail was present in any of the remains. The basal parts of the plant are unknown.

Discussion. Edwards and Richardson (1974) erected the form genus *Salopella* to distinguish compression fossils having *Rhynia*-like sporangial shape and naked dichotomizing axes from the much better-preserved plants from the Rhynie Chert. It is clear that this new species belongs in the form genus, but there are differences from the type species *S. allenii*, and from *Rhynia*. There are other characters which are common to both the new *Salopella* and other members of the Rhyniaceae.

There are seven genera in the family Rhyniaceae (*sensu* Banks 1975). Of these, five have sporangia with height exceeding the width. *Rhynia* and *Salopella* are in this group, as are *Horneophyton lignieri* (Kidston and Lang) Barghoorn and Darrah, *Steganotheca striata* Edwards, and *Eogaspesia gracilis* Daber.

Eogaspesia from the Gaspé Peninsula, Quebec is a gregarious plant with small oval sporangia (Daber 1960). The narrow axes rarely branch and its bushy habit readily distinguishes it from *Salopella australis*. *Horneophyton lignieri* has small cylindrical sporangia with a distinct columella. There is no indication of such tissue preserved in *Salopella*. *Steganotheca striata* Edwards (1970) has truncated fusiform sporangia and a branching habit whereby the tips of the branches are parallel, a branching pattern (see Edwards 1970, Pl. 84, fig. 1.2) closely resembling the branching illustrated for *Salopella australis* in Plate 32, figs. 1–5. *Steganotheca striata* also has axes which gently taper to increase in diameter below the sporangia so that the sporangial bases are not clearly defined; the sporangia are small (1.8 mm) and cup shaped.

The dimensions of the sporangia and axis width of the new *Salopella* are almost exactly the same as those of *Rhynia major*. *R. gwynne-vaughani* has smaller sporangia which abscise, protuberances on the axes and an adventitious branching system. From the descriptions of Kidston and Lang (1917 and 1920), it appears that *R. major* not only does not branch as frequently as *Salopella*, but also has axes tapered from 6 mm at their bases to 1.5 mm below the sporangia. Both *Rhynia* species have clearly defined sporangial bases and although *R. major* has some sterile tissue at the apex of the sporangium (Kidston and Lang 1917, Pl. 9, fig. 62), it is not extensive. Although it is difficult to compare impression fossils with petrifications, *R. major* appears to have the broadest part of its sporangium about one-third its length from the base, the upper two-thirds tapering slightly to a rounded apex.

The sporangia of *S. allenii* also differ from those of the new species. Although the dimensions of the sporangia are the same, *S. allenii* has true fusiform sporangia, compared to the parallel-sided ones of the new *Salopella*. *S. allenii* sporangia lack the defined spore area as seen on most specimens of *S. australis*; the sporangial bases of *S. allenii* are more clearly defined and their axes dichotomize directly below the sporangia. This character was observed only once (Pl. 32, fig. 4) in the Victorian specimens.

The new *Salopella* is a larger plant in terms of axis length and does not dichotomize as frequently as *S. allenii*, although it is important to note that *S. allenii* is known from only one specimen.

Another genus with terminal oval sporangia which is known in Victoria is *Sporogonites*. Halle (1916), in his diagnosis of *Sporogonites*, described the sporangium as 'a capsule obovoid or clavate' with a slender rigid stalk. The stem broadens to form the basal region of the capsule. *Sporogonites* has a possible central horizontal line of dehiscence, longitudinal ridges, and is not regarded as being a

vascular plant (Andrews 1960). A Victorian species, *S. chapmani*, is known from the late Early Devonian (Emsian) Walhalla Group (Lang and Cookson 1930). Cookson (1949) reported *S. sp.* from the Ruddock Siltstone which may be equivalent to, or slightly younger than the Wilson Creek Shale. *Sporogonites* has not been reported from the Wilson Creek Shale, and *S. chapmani* is quite distinct when compared with *Salopella australis* in terms of axis width and sporangial shape and size.

Edwards and Richardson (1974) comment on the similarity of *S. allenii* sporangial shape to that of another Victorian genus, *Hedeia corymbosa* (Cookson 1935). They point out that *H. corymbosa* has a more compact fructification, with up to four orders of branching in a comparatively short length of axis.

A period of at least 20 million years probably separates the two deposits in which *S. australis* is found, but there is no evidence at present to suggest that changes have occurred in the species over this interval. Specimens collected from the older beds at Limestone Road tend to have longer axes. Although the plant remains at Frenchman Spur have been further fragmented by the close jointing pattern at the site, they were probably of shorter lengths than those at Limestone Road at the time of deposition.

While no anatomy is preserved in the new *Salopella*, from the gross morphology it would appear that the fertile portion of *S. australis* may be little more than a zone of the shoot apex in which spores develop, and it therefore lacks an organ that could be clearly defined as sporangium. If this proves to be so, it may represent the most primitive sporangial condition known amongst the early land plants. The small indentation noted in some specimens may indicate a position where the apex breaks off to release the spores. From the faint lines and ridges in two specimens it is presumed that this plant was vascularized.

Because of the small differences in branching and sporangial shape, and the geographical separation between this species and *S. allenii*, it seems advisable to erect a new species with the specific name '*australis*' for the southern hemisphere plant.

Salopella caespitosa sp. nov.

Plate 33, figs. 1-4; Plate 34, fig. 3; text-fig. 2D

Diagnosis. Tufted plant at least 85 mm high of slender naked axes 1.2 mm wide, bearing ovate to fusiform sporangia averaging 4.5 mm long and 1.7 mm wide. There are up to three orders of branching, the ultimate dichotomy normally at least 25 mm below the sporangia, but occasionally at the sporangial base.

Range. Pragian.

Type locality. Frenchman Spur.

Horizon. Wilson Creek Shale.

Holotype. NMV P50,016. Plate 33, figs. 1-4; Plate 34, fig. 3.

Derivation of specific name. '*caespitosa*'—tufted.

Description. The diagnosis is based on one specimen, part and counterpart. Preservation is poor, with little mineral remaining except on some sporangia and an occasional fine line along the centre of the axis. A brittle film of almost transparent mineral is all that remains of most of the axes and the exterior part of the sporangia.

The plant consists of a number of axes, in excess of 20. The axes do not taper but after each dichotomy decrease in diameter. They cross each other and disappear into the matrix, making it impossible to follow fertile axes to the bottom of the specimen, and axes from the lower parts to their apices. The broadest axis on the specimen measures 1.9 mm, while the lowest portion of axis known to terminate in sporangia (sporangia 1-3, see Pl. 33, figs. 1, 2) has a width of 1.7 mm. After three orders of branching, this width decreases to 1.1 mm. When axes can be traced to termination, all appear to be fertile. Many axes show a fine central line 0.2 mm wide, presumably the remains of the vascular trace. The angles of branching are narrow (10-45°), although the extremes of this range may be an artefact of preservation.

There are twenty-six sporangia visible in the part and counterpart (see Pl. 33, fig. 1), although some of these are

incomplete. The sporangia range from ovate to fusiform in shape, the larger being more fusiform and the smaller ovate. The size ranges from 3.2–6.0 mm (average 4.5 mm) in length and 1.3–2.0 mm (average 1.7 mm) at the widest point. The longest sporangia are not always the broadest. Three axes probably have more than one sporangium at their apices (Pl. 33, figs. 3, 4). Sporangium 13, illustrated in Plate 33, fig. 3, appears to have two sporangia, partially superimposed. The tops of them have been broken away but Plate 33, fig. 4, illustrating the counterpart, has the apices visible. Sporangium 14 is also broader than other single sporangia. The presumed vascular trace of the axis of sporangium 15 appears to divide at the base of the sporangium. The preservation is not good enough to determine whether the trace actually goes to two presumed spore bodies, or even three. Sporangia 13, 14, and 15 are all in close proximity, although their axes do not appear connected. These are the only axes which appear to divide so close to the base of their sporangia.

Of the intact axes, none was seen to terminate in a sterile tip. Variation in sporangial shape could be due to the stage of maturity of the sporangia, the longer and more fusiform (e.g. sporangia 6–9) possibly being less mature. It is recognized also that sporangia 13–15 could be the result of the manner of preservation, either in compression to give a broader appearance to a single sporangium, or by superimposition, as shown by the axes of sporangia 5 and 6. However, the axes of sporangia 13 and 14 remain as one for their entire length, so it appears unlikely that superimposition has occurred. Similarly, it seems unlikely that squashing and spreading should only happen to these sporangia. It is also possible that they are at a stage of dehiscence, with the sporangial wall breaking away (see especially sporangium 14; Pl. 33, fig. 1). As the axes of these sporangia are broader (1.6, 1.5, and 1.5 mm respectively) just below the sporangial base than any other axis at the same point, it appears that each axis supports two sporangia.

Surrounding most of the dark spore bodies is a deposit of the semi-transparent mineral (e.g. sporangia 1–3, 7, 8, and 10). No spores could be isolated from the presumed spore bodies, nor could any line of dehiscence be seen. Basal parts of this plant are unknown and the tufted habit is assumed on the basis of the orientation of the axes as preserved.

Discussion. It may be inferred from this specimen of semi-aligned axes that they are all from the one plant, arising perhaps from a rhizome or gametophyte. Fragments of axes of comparable diameter from the Wilson Creek Shale are rare. It appears that this species was either more delicate and hence unable to survive a long period of immersion, or that the plant was less abundant than other Victorian rhyniophytes.

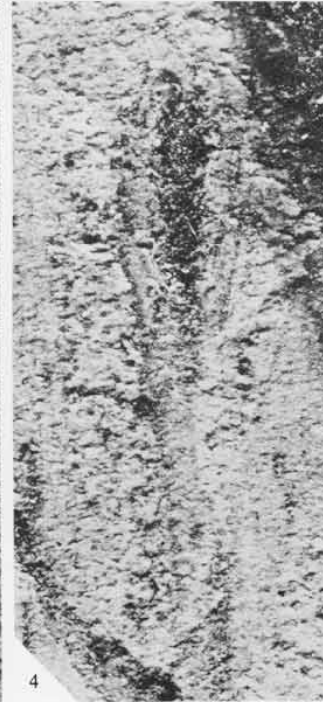
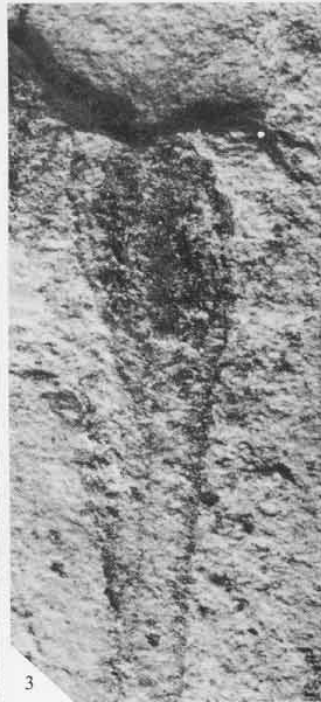
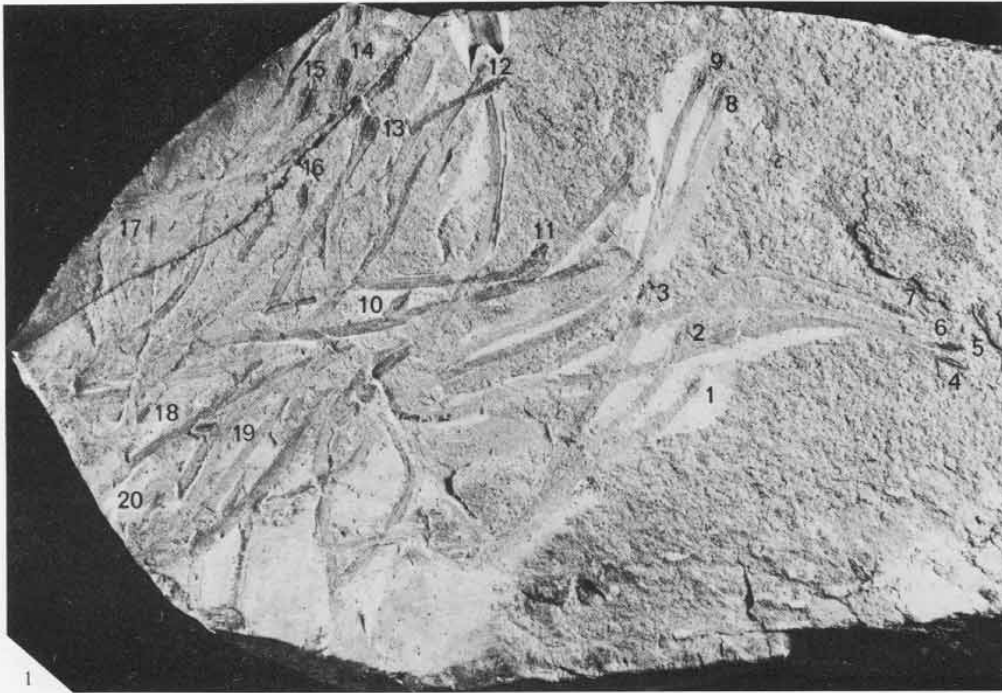
The points made in the discussion on *Salopella australis* are also relevant here. In habit the plant resembles several northern hemisphere Early Devonian plants—*Steganotheca striata*, *Renalia hueberi* Gensel, and *Eogaspesia gracilis*. *Hicklingia edwardii* Kidston and Lang from the Middle Devonian is also similar in appearance. *Hicklingia* is considered a zosterophyll on the basis of its sporangial arrangement (Edwards 1976). Gensel (1976) considers *Renalia* to be intermediate between the Rhyniophytina and the Zosterophyllophytina. *Eogaspesia* has few fertile axes and the sporangia are elliptical rather than ovate; the axes rarely dichotomize and the genus is thought by Höeg (1967) and Gensel (1976) to be non-vascular.

Rhynia gwynne-vaughani has sporangia only slightly smaller and of similar shape to the tufted plant we have described as *Salopella caespitosa*. The habit of *R. gwynne-vaughani* (see Edwards 1980) is distinct, with adventitious branching. As is the case with *S. australis*, *S. caespitosa* cannot be compared adequately with the well-described genus *Rhynia*, and is more appropriately placed in the form genus *Salopella*.

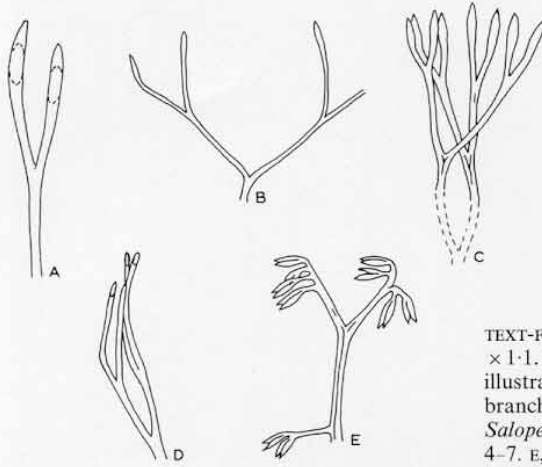
More is known of the habit of *S. caespitosa* than of the type species *S. allenii*. They both differ from *S. australis* in sporangial size and in having a definite base to the sporangium. *S. australis* axes are

EXPLANATION OF PLATE 33

Figs. 1–4. *Salopella caespitosa* sp. nov.; holotype; NMV P50,016. 1, complete specimen (part) showing numbered sporangia (refer to text); Frenchman Spur; $\times 1$. 2, branching in *S. caespitosa*; stems bearing sporangia nos. 4–7 (part); see also text-fig. 2D; $\times 1.1$. 3 and 4, part and counterpart of sporangium 13; fig. 3 shows the stem with the remains of the presumed vascular trace; this sporangium gives the appearance of being double; however, the counterpart (fig. 4) does not show this nearly as well; $\times 10$.



TIMS and CHAMBERS, *Salopella*



TEXT-FIG. 2. A, *Salopella australis*, diagram of holotype, $\times 1.1$. B, *S. australis*, diagram of large branched specimen illustrated in Pl. 32, fig. 5, $\times 0.5$. C, *S. australis*, possible branch structure of specimen illustrated in Pl. 32, fig. 3. D, *Salopella caespitosa*, branching of axis bearing sporangia 4-7. E, *Dawsonites subarcuatus*, reconstruction.

broader, have wider branch angles, and the fragmentary nature of the remains suggests that it may not have been a gregarious plant.

The possible development of two sporangia terminating the one axis as in *S. caespitosa* may indicate a higher level of organization towards more complex Rhyniophytina with multisporangiate terminal fructifications, such as *Yarravia* and *Hedeia*. *Y. oblonga* is found with both species of Australian *Salopella* at Frenchman Spur. However, an as yet undescribed *Hedeia* is present in the Ludlovian Lower Plant Assemblage. If the organization seen in *Hedeia* evolved from the simpler organization of *Salopella*, this must have occurred earlier than the Ludlovian.

Subdivision TRIMEROPHYTINA Banks 1968

Genus DAWSONITES Halle 1916

Type species. *D. arcuatus*.

Dawsonites subarcuatus sp. nov.

Plate 34, figs. 1, 2; text-fig. 2E

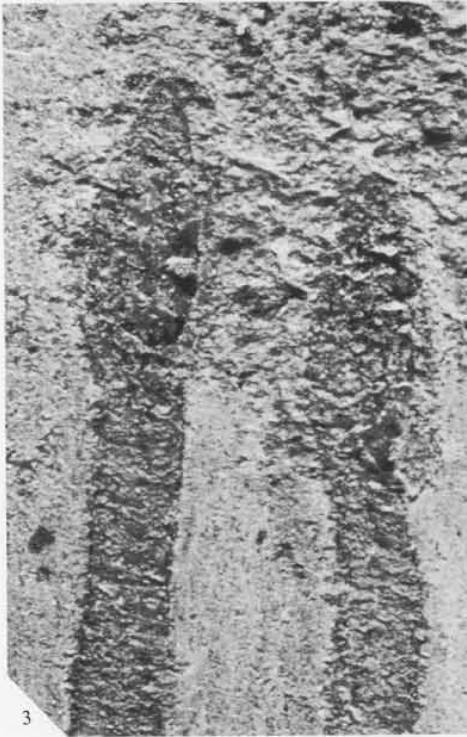
Diagnosis. Dichotomizing branch system with sympodially formed main axis due to dominance of the leading branch. Ultimate branches tapering, and bearing at the apex of each dichotomy narrow, straight, lanceolate sporangia, 3-4 mm long.

EXPLANATION OF PLATE 34

Figs. 1, 2. *Dawsonites subarcuatus*; NMV P33,215; part and counterpart. Specimen with one pseudomonopodial branch near the base and ultimate dichotomous branching; at least four sporangia are present on the left branch (fig. 2) and six on the right; counterpart shows the central line down the axis, the presumed vascular trace (arrow); Frenchman Spur; $\times 4.5$.

Fig. 3. *Salopella caespitosa*; NMV P50,016; sporangia 8 (right) and 9; sporangium 9 shows the clear delineation of the sporangial wall; $\times 15$.

Figs. 4, 5. NMV P50,013; *Salopella australis*; counterpart and part; part shows the dark presumed sporogenous area, whilst the counterpart has no such dark area; Frenchman Spur; $\times 1.7$.



TIMS and CHAMBERS, *Dawsonites* and *Salopella*

Range. Early Devonian (Pragian).

Type locality. Frenchman Spur.

Horizon. Wilson Creek Shale.

Holotype. NMV P33,215a and b. Plate 34, figs. 1, 2.

Derivation of specific name. 'subarcuatus': 'sub'—somewhat or almost, 'arcuatus'—curved like a bow.

Description. This is based on a single specimen from Frenchman Spur, part and counterpart of a plant of a form not previously recorded from Australia but closely resembling *D. arcuatus* Halle. Overall the specimen measures 18 mm in length. The naked axis branches at four levels, the first unequally 1.5 mm from the base of the specimen, at an angle of almost 90°. A further 9 mm up the axis is a dichotomy with a 70° angle between the forks. The axis itself is 1 mm broad at the base and narrows to 0.7 mm at the dichotomous branching. A further branching occurs on one fork of the dichotomy (the right fork of P33,215a, shown in Pl. 34, fig. 1, shows this best), to give two groups of sporangia (see also text-fig. 2E). Because of the manner of preservation the actual point of branching cannot be seen. The fourth level of branching takes place 0.7 mm below the sporangia. The stem has a central strand, about 0.2 mm wide, visible as a ridge of thicker carbon in P33,215a and a corresponding depression in the counterpart. The ridge branches with the axis and is the presumed remains of the vascular trace.

All the branches terminate in elongate fusiform sporangia which point to the left of the axis (right in the counterpart). This is probably a depositional effect and in life the sporangia may have been semi-pendent. Each branch divides to carry at least three sporangia on separate stalks, except for one which bears two sporangia on the one stalk. Whole sporangia are 3–4 mm long and 0.4–0.7 mm broad. Sporangia of the first branch are absent from the counterpart. No obvious lines of sporangial dehiscence are shown. Cellulose acetate film pulls of the sporangia yielded no spores.

Discussion. When Halle (1916) erected the genus *Dawsonites* for fragments of branched axes with terminal recurved pairs or groups of sporangia, he was aware of their close similarity to sporangia assigned to *Psilophyton princeps* by Dawson (1859, 1871). However, because of the lack of physical connection between the spiny axes and the terminal sporangia of the northern hemisphere species, *P. princeps*, Halle considered a new genus was justified for the specimens he found in Norway. The two taxa, *D. arcuatus* and *P. princeps*, have been proved by Hueber and Banks (1967) to be conspecific. However, in the intervening period *Dawsonites* has become a form genus for fragmentary axes bearing terminal sporangia. Banks *et al.* (1975) state that *Dawsonites* should be used in Halle's restricted sense rather than that of Høeg (1967), who cited eight species and widened the concept of the genus. The Wilson Creek Shale specimen fits into the original description of the genus.

The resemblance of specimen P33,215 to Halle's original *D. arcuatus* is quite apparent. There are, however, a number of minor differences. The sporangia of P33,215 do not droop from recurved branches but hang, probably semi-pendently, from straight branches which dichotomize at a wider angle than those of *D. arcuatus*. Also, the sporangial shape differs slightly, most sporangia being more elongate in the Victorian specimen. There are no ridges on the stem, although this feature may have been lost in preservation. Spines, which are a characteristic of *P. princeps* and also of the lower portions of some of the specimens identified as *D. arcuatus* in the Northern Hemisphere, are absent from the Victorian specimen. This may be because the specimen is such a small fragment and spines could have been present further down the axis. Spiny axes are rare in the Victorian Lower Devonian. Cookson (1935) recorded some non-fertile spiny axes from the Mt. Pleasant Sandstone and we have collected some recently from the Frenchman Spur locality.

Psilophyton axes also have pseudomonopodial branching, and a few specimens of naked axes from other Early Devonian strata of Victoria have been found with branching of this type. At present, however, there is no evidence that the fertile specimen and the axes are related.

It is recognized that if more material comes to hand this specimen may be reassigned to another genus. The specimen resembles *D. arcuatus* in size and overall form extremely closely. It fits well into Halle's diagnosis for *Dawsonites*, 'sporangium bearing branch systems, dividing dichotomously, or differentiated into a sympodially formed main axis and bifurcating lateral branches. Ultimate

branches slender and curved, bearing terminal capsules of a narrowly obovoid or short fusiform shape and usually 3–5 mm long.' It is the only representative of the subdivision Trimerophytina yet found in the Victorian early land flora. This record of a trimerophyte in the Victorian Siegenian is contemporaneous with the first appearance of the group in the Northern Hemisphere.

The geographic separation of Halle's species from Norway and those in south-eastern Australia, together with their minor differences mentioned above, have led to the designation of this specimen as a new species, *D. subarcuatus*.

GENERAL CONCLUSIONS

The Lower Plant Assemblage

The Lower Plant Assemblage contains, in addition to *Salopella australis*, *Baragwanathia longifolia*, a new species of *Hedeia*, a new genus from the Zosterophyllophytina, and other unidentified fragmentary remains. Only three species, *S. australis*, *B. longifolia*, and the new *Hedeia* are common to both the Lower Plant Assemblage and the Wilson Creek Shale. The Wilson Creek Shale contains other species as mentioned previously. In other words, the floras are quite distinct, having a minority of species in common. Even in *B. longifolia*, there are some small differences in form—this will be discussed fully elsewhere.

We recognize that the dating of the Lower Plant Assemblage as Ludlovian is controversial, and has already been questioned (Edwards *et al.* 1979; Hueber 1983). We also acknowledge our own caution as to the age. The two pre-Devonian floras of Wales (Edwards 1979; Edwards and Rogerson 1979) and Podolia (Obrhel 1962) from the Northern Hemisphere consist of simple, tiny plants in comparison. There is, however, mounting evidence on the associated graptolites that the Lower Plant Assemblage is indeed Ludlovian. Recent studies (Rickards and Garratt, pers. comm.) have shown there are two Ludlovian genera of graptolites.

Palaeogeographic maps of the Early Devonian (Smith *et al.* 1973; Heckel and Witzke 1979) show Europe and Australia in equatorial regions on opposite sides of the globe. Is it possible that the flora could have developed in isolation 20,000 km from the *Cooksonia* floras of Wales and Podolia? *Cooksonia*-type plants were present in the Wenlockian in Ireland (Edwards and Feehan 1980) but little development in vascular plant form seems to have occurred in Europe until the beginning of the Devonian. Did a period of rapid evolution occur in the flora of the Melbourne Trough, and was it contained there until the Early Devonian? The only possible vascular plants older than the Lower Plant Assemblage currently known in Victoria are found as *Hostinella*-type chaff about 180 m stratigraphically below the Lower Plant Assemblage and in the same district. There is no sign of *Baragwanathia* in the chaff, despite the fact that *Baragwanathia* is easily recognized even in small fragments.

The Early Devonian

The three new species described here are from genera previously recorded only from the Northern Hemisphere. Edwards (1973) considers that there were two contrasting floras in the Early Devonian, one being that of the Northern Hemisphere and Australia, and the other restricted to the southern hemisphere continents: South America, southern Africa, and Antarctica. While it must be remembered that *Salopella* and *Dawsonites* are form genera only and may not be genetically related to their northern hemisphere counterparts, they come, with *Zosterophyllum*, from three separate subdivisions. The presumed non-vascular *Sporogonites* and *Pachytheca* are common to both the Northern Hemisphere and Australia. *Baragwanathia* is very similar to the northern hemisphere genus *Drepanophycus* and, indeed, a new species of *Baragwanathia* from Canada has been described by Hueber (1983). These records must be considered as strong evidence to support the link between the floras of Australia and the Northern Hemisphere during Early Devonian times. This evidence also suggests that some mixing of the floras had occurred before the Pragian.

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REFERENCES

- ANDREWS, H. N. 1960. Notes on Belgian specimens of *Sporogonites*. *Palaeobotanist*, **7**, 85–89.
- BANKS, H. P. 1968. Early history of land plants. In DRAKE, E. T. (ed.). *Evolution and Environment*. Yale Univ. Press, Newhaven. Pp. 73–107.
- 1975. Reclassification of Psilophyta. *Taxon*, **24**, 401–413.
- LECLERCQ, S. and HUEBER, F. M. 1975. Anatomy and morphology of *Psilophyton dawsonii* sp. n. from the late Lower Devonian of Quebec (Gaspé) and Ontario, Canada. *Palaeontogr. am.* **8**, 77–127.
- COOKSON, I. C. 1935. On plant remains from the Silurian of Victoria, Australia, that extend and connect floras hitherto described. *Phil. Trans. R. Soc., Ser. B*, **225**, 127–148.
- 1949. Yeringian (Lower Devonian) plant remains from Lilydale, Victoria, with notes on a collection from a new locality in the Siluro-Devonian sequence. *Mem. natn. Mus. Vict.* **16**, 117–131.
- COUPER, J. 1965. Late Silurian to Early Devonian stratigraphy of the Yea–Molesworth district, Victoria. *Proc. R. Soc. Vict.* **79**, 1–8.
- DABER, R. 1960. *Eogaspesia gracilis* n.g., n.sp. *Geologie*, **9**, 418–425.
- DAWSON, J. W. 1859. On fossil plants from the Devonian rocks of Canada. *Q. Jl geol. Soc. Lond.* **15**, 477–488.
- 1871. *The fossil plants of the Devonian and Upper Silurian formations of Canada*. Geological Survey of Canada. 92 pp.
- EDWARDS, D. 1970. Fertile Rhyniophytina from the Lower Devonian of Britain. *Palaeontology*, **13**, 451–461.
- 1973. Devonian Floras. In HALLAM, A. (ed.). *Atlas of Palaeobiogeography*. Elsevier, Amsterdam. Pp. 105–115.
- 1976. The systematic position of *Hicklingia edwardii* Kidston and Lang. *New Phytol.* **76**, 173–181.
- 1979. A Late Silurian flora from the Lower Old Red Sandstone of south-west Dyfed. *Palaeontology*, **22**, 23–52.
- BASSETT, M. G. and ROGERSON, E. C. W. 1979. The earliest vascular land plants: continuing the search for proof. *Lethaia*, **12**, 313–324.
- and FEEHAN, J. 1980. Records of *Cooksonia*-type sporangia from late Wenlock strata in Ireland. *Nature*, **287**, 41–42.
- and RICHARDSON, J. B. 1974. Lower Devonian (Dittonian) plants from the Welsh borderland. *Palaeontology*, **17**, 311–324.
- and ROGERSON, E. C. W. 1979. New records of fertile Rhyniophytina from the Late Silurian of Wales. *Geol. Mag.* **116**, 93–98.
- EDWARDS, D. S. 1980. Evidence for the sporophytic status of the Lower Devonian plant *Rhynia gwynne-vaughani* Kidston and Lang. *Rev. Palaeobot. Palynol.* **29**, 177–188.
- GARRATT, M. J. 1978. New evidence for a Silurian (Ludlow) age for the earliest *Baragwanathia* flora. *Alcheringa*, **2**, 217–224.
- 1981. The earliest vascular land plants. Comment on the age of the oldest *Baragwanathia* flora. *Lethaia*, **14**, 8.
- GENSEL, P. G. 1976. *Renalia hueberi*, a new plant from the Lower Devonian of Gaspé. *Rev. Palaeobot. Palynol.* **22**, 19–37.
- HALLE, T. G. 1916. Lower Devonian plants from Rörågen in Norway. *K. svenska Vetensk.Akad. Handl.* **57**, 1–46.
- HARRIS, W. J. and THOMAS, D. E. 1941. Notes on the Silurian rocks of the Yea district. *Min. geol. J. Vict.* **2**, 302–304.
- HECKEL, P. H. and WITZKE, B. J. 1979. Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators. In HOUSE, M. R., SCRUTTON, C. T., and BASSETT, M. G. (eds.). *The Devonian System. Spec. Pap. Palaeont.* **23**, 99–123.
- HÖEG, O. A. 1967. Psilophyta. In BOUREAU, F. (ed.). *Traité de Paléobotanique*. Masson et Cie, Paris.
- HUEBER, F. M. 1983. A new species of *Baragwanathia* from the Sextant Formation (Emsian) Northern Ontario, Canada. *J. Linn. Soc. (Bot.)*, **86**, 57–79.
- and BANKS, H. P. 1967. *Psilophyton princeps*: the search for organic connection. *Taxon*, **16**, 81–85.

- JAEGER, H. 1966. Two late *Monograptus* species from Victoria, Australia and their significance for dating the *Baragwanathia* flora. *Proc. R. Soc. Vict.* **79**, 393-413.
- 1970. Remarks on the stratigraphy and morphology of Pragian and probably younger monograptids. *Lethaia*, **3**, 173-182.
- KIDSTON, R. and LANG, W. H. 1917. On Old Red Sandstone plants showing structure, from the Rhynie Chert bed, Aberdeenshire. Part I. *Rhynia Gwynne-Vaughani*, Kidston and Lang. *Trans. R. Soc. Edinb.* **51**, 761-784.
- 1920. On Old Red Sandstone plants showing structure, from the Rhynie chert bed, Aberdeenshire. Part II. Additional notes on *Rhynia Gwynne-Vaughani*, Kidston and Lang; with descriptions of *Rhynia major*, n. sp., and *Hornea lignieri* n.g., n. sp. *Ibid.* **52**, 603-627.
- KOREN', T. N. 1971. The zones of *Monograptus hercynicus* and *Monograptus falcarius* in Pai-Khoi. *Lethaia*, **4**, 235-248.
- LANG, W. H. and COOKSON, I. C. 1930. Some fossil plants of Early Devonian type from the Walhalla Series, Victoria, Australia. *Phil. Trans. R. Soc. Lond., Ser. B.*, **219**, 133-163.
- 1935. On a flora, including vascular land plants, associated with *Monograptus*, in rocks of Silurian age, from Victoria, Australia. *Ibid.* **224**, 421-449.
- MOORE, B. R. 1965. The geology of the Upper Yarra region, central Victoria. *Proc. R. Soc. Vict.* **78**, 221-239.
- OBRHEL, J. 1962. Die Flora der Pridoli Schichten (Budnany-Stufe) des mittelböhmisches Silurs. *Geologie*, **11**, 83-97.
- SCHOPF, J. M. 1975. Modes of fossil preservation. *Rev. Palaeobot. Palynol.* **20**, 27-53.
- SMITH, G., BRIDEN, J. C. and DREWRY, G. E. 1973. Phanerozoic World Maps. In HUGHES, N. F. (ed.). *Organisms and Continents through Time. Spec. Pap. Palaeont.* **12**, 1-42.

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