



A Late Devonian refugium for *Colpodexylon* (Lycopsida) at high latitude

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ABSTRACT

Localities within strata of the Witpoort Formation (Witteberg Group, Cape Supergroup) of South Africa provide diverse new fossil material of Famennian plants from a high palaeolatitude marginal marine setting. Lycopsid axes with sterile leaves include material here diagnosed to two new species of *Colpodexylon* Banks 1944. *C. pullumpedes* sp. nov. from Waterloo Farm is a 'short-tipped' species, whereas *C. mergae* sp. nov. from Coombs Hill, is a 'long-tipped' species. The latter has leaves similar to those of the type species, *C. deatsii* Banks, yet differing in proportions. This provides the first definite high latitude records of the genus. Furthermore, these occurrences substantially extend the temporal range of *Colpodexylon*, formerly only known from lower Frasnian and older strata, indicating that the genus persisted at high-latitudes after its apparent disappearance from the palaeo-sub-tropics.

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1. Introduction

Colpodexylon was first described by Banks (1944), who identified it as a herbaceous lycopod having a characteristic lobed xylem strand and bearing three-tipped microphyllous leaves, with sporangia borne on the upper surface of unmodified leaves.

Banks assigned the genus to Protolopodiales, a primitive lycopod order, which includes most of the herbaceous lycopod taxa known from the Middle Devonian (Bonamo et al., 1988; Gensel and Berry, 2001). Most genera of this order are thought to have disappeared during the Frasnian or earlier (Berry and Edwards, 1996; Gensel and Berry, 2001; Meyer-Berthaud et al., 2003). Occurrences of *Frenguella* Arrondo et al. 1991 in the Lower Carboniferous of Argentina, however, indicate that the order might have survived the end of the Devonian (Gensel and Berry, 2001; Prestianni et al., 2015).

Protolopodiales occurred worldwide in the Middle Devonian and are represented in southern high-palaeolatitude regions by *Haskinsia* Grierson and Banks 1963 and '*Haplostigma*' Seward 1932 (Cingolani et al., 2002; Xu and Berry, 2008). The group may have been more diverse in southern Gondwana than is apparent as '*Haplostigma*' probably includes species from a variety of protolopodialean genera (Cingolani et al., 2002). The possibility that *Colpodexylon* extended into high latitudes was suggested by resemblance of a paratype of '*Haplostigma*' from the Upper Devonian of South Africa to *Colpodexylon* (V.236, Natural History Museum, London), although a positive

identification is precluded by the specimen's incompletely preserved leaves (Cingolani et al., 2002). Fossil material, herein described, confirms the presence of *Colpodexylon* in South African Famennian strata. The taxonomy and palaeobiogeographic implications of the new species are explored below.

2. Material and methods

2.1. Provenance of fossil specimens

Specimens described here were collected at two localities within the Witpoort Formation (Witteberg Group, Cape Supergroup) (Fig. 1). The age of the formation was originally determined on the basis of correlation to the global sea level curve of Johnson et al. (1985), its lower and upper boundaries corresponding roughly to those of the Famennian Stage (Cooper, 1986). Placement of the Devonian–Carboniferous boundary at the top of the Witpoort Formation is in accordance with vertebrate biostratigraphy (Gess, 2016) and palynology of overlying Lower Carboniferous aged strata (Stroel and Theron, 1999).

Colpodexylon pullumpedes sp. nov. comes from the Waterloo Farm *lagerstätte*, exposed in a road cutting to the south of Grahamstown/Makhanda (Fig. 1A). This horizon is stratigraphically near the top of the Witpoort Formation and is late Famennian in age (Gess, 2016). Sedimentological studies of the locality indicated a back-barrier, brackish water lagoonal deposit, along a high energy coastline (Hiller and Taylor, 1992). Subsequent palaeontological research is consistent with this interpretation as the assemblage includes both marine algae (Hiller and Gess, 1996) and non-marine charophyte algae

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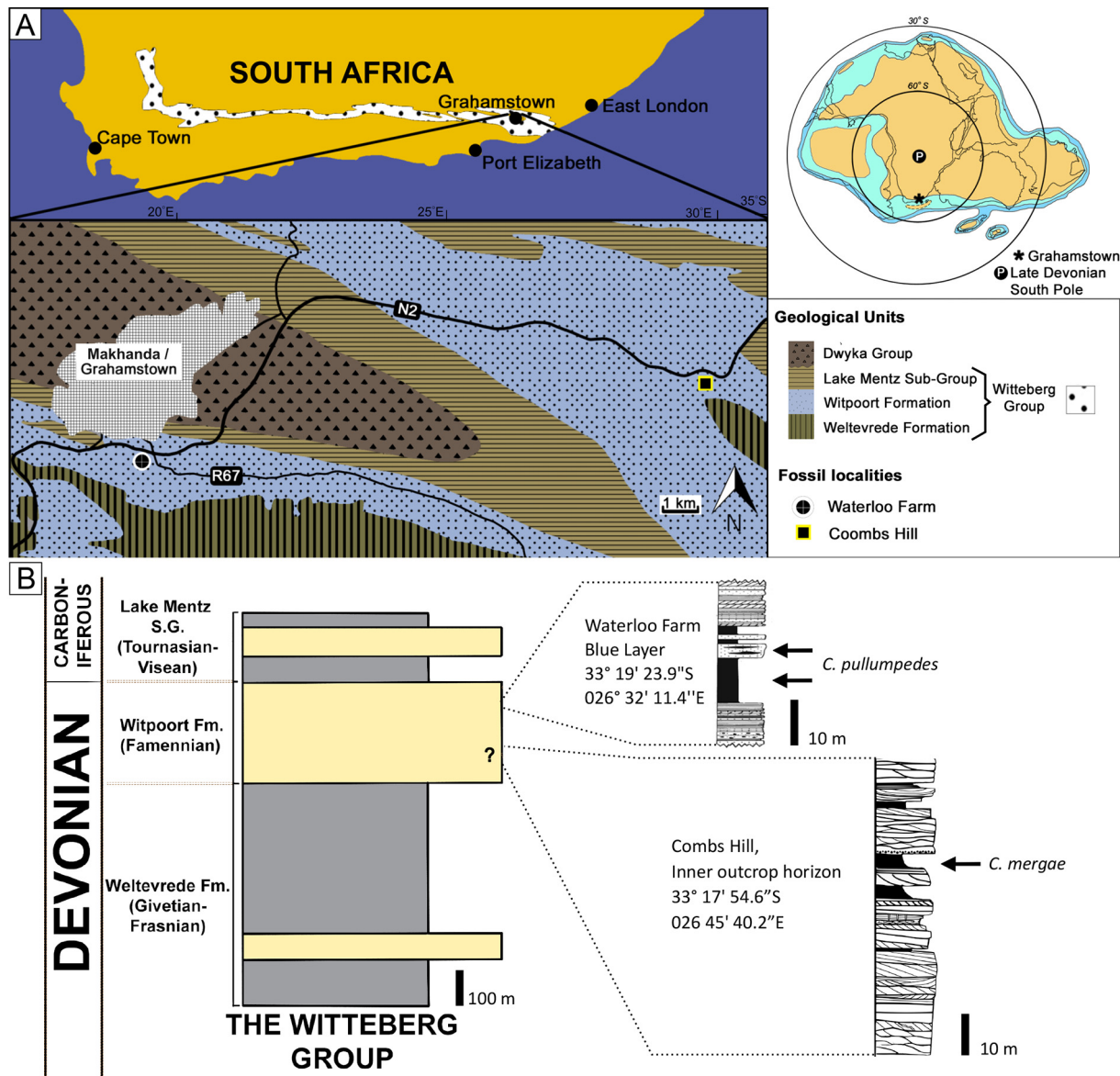


Fig. 1. Locality and stratigraphic setting of Coombs Hill and Waterloo Farm. **A)** Geological map (based on Council for Geoscience sheet 3326, 1:250,000) showing the relevant fossil localities. Palaeogeographic reconstruction for the Famennian modified from Gess and Ahlberg (2018) shown at top right. **B)** Sedimentary logs for the horizons of the two new species of *Colpodexylon*, the Waterloo Farm section modified from Hiller and Taylor (1992) and the Coombs Hill section modified from Harris et al. (2021).

(Gess and Hiller, 1995a), an estuarine fauna (Gess and Whitfield, 2020) and a terrestrial flora. Terrestrial plants include the heterosporous lycopods *Kowieria alveoformis* Gess and Prestianni, 2018 and *Leptophloeum rhombicum* Dawson 1862 (Prestianni and Gess, 2014), *Archaeopteris notosaria* Anderson et al. 1995, a sphenophyte *Rhinistachya riniensis* Prestianni and Gess 2018, a putative iridopteridalean (Gess and Prestianni, in prep), and various undescribed species (Gess and Hiller, 1995b).

Two specimens of *C. pullumpedes* were recovered during roadworks in 2007 from the Blue Layer, a thick black shale approximately 100 m westward along strike from the Main Fish Lens (MFL; Gess and Prestianni, 2018). One came from a loose block of black shale derived from the Blue Layer (Co-1) and the other (Co-2) from sandier sediments immediately overlying the black shale. Metre-scale stratigraphy of this locality was recorded by Hiller and Taylor (1992).

Colpodexylon mergae sp. nov. was collected from a new locality on a north-facing ridge bordering the Coombs valley, 21 km east of Waterloo

Farm (Fig. 1). The Coombs Hill locality was discovered late in 2015 during road upgrades along the N2 national highway. An enormous roadcutting intersected a hill of quartzitic sandstones, in which laterally extensive lenses of carbonaceous grey mudstone, bearing abundant fossil plant remains, were investigated.

All *Colpodexylon* identified at Coombs Hill were recovered from the 'Inner Outcrop', the stratigraphically second highest of four mudstone marker beds in the cutting section (the upper portion of which is shown in Fig. 1). The Inner Outcrop comprises a 2–3 m thick layer of stratified grey and reddish mudstone with poor fissility, which is interpreted as representing a brackish water lagoonal setting (Harris et al., 2021).

Coombs Hill and Waterloo Farm occur on opposite limbs of the Grahamstown synclinorium, and their precise stratigraphic relationship is, as yet, unresolved. This is largely due to intense structural deformation which has inhibited stratigraphic work in the region. This formation has yielded no microfossils, which also hinders stratigraphic correlations.

2.2. Preservation and study of specimens

Fossil specimens are preserved as flattened compressions in carbonaceous grey to black clay/silt matrix. Usually, the protolepidodendrolean axes preserve outer cortical impressions filled internally by matrix, and compressed, so that the fossil comprises impressions of lower and upper internal or external cortical surfaces separated by a thin wafer of sediment. Organic material was altered to a white phyllosilicate mineral during low-grade metamorphism and tectonic uplift (Gess and Hiller, 1995b).

The rock matrix often parts at the level of the stem, where the coarsest fossil material has created a weakness. If leaves are attached, they are usually visible only along the margins of the stem. Elongate leaves such as those herein described generally require further preparation to expose their full extent. Conventional techniques of *dégagement* were used (Fairon-Demaret et al., 1999), however, on some specimens from Coombs Hill, the soft clay matrix tended to smear rather than flake under sharpened needles, and therefore, leaves were uncovered using 3–5 mm wide flat head chisels and a light hammer. Fine preparation was performed under a Zeiss Stemi 408 binocular microscope with cross-polarized illumination. Photographic enlargements of leaves were attained with an attached Zeiss Axiocam 105 colour camera. Fossils were photographed using a Nikon DSLR camera, and line drawings were made by tracing photographs using Adobe Photoshop CC 2018, in continual consultation with the material.

2.3. Repository

All fossil specimens are housed at the Albany Museum, Devonian Lab in Grahamstown/Makhanda.

3. Systematics

Class: LYCOPSIDA Pichi-Sermolli 1958

Order: PROTOLEPIDODENDRALES Pichi-Sermolli 1958

Family: PROTOLEPIDODENDRACEAE Kräusel and Weyland 1949

Genus: **Colpodexylon** Banks, 1944 emend. Berry and Edwards, 1995

Type species: *Colpodexylon deatsii* Banks, 1944

Colpodexylon pullumpedes species nova:

Etymology: pullumpedes from Latin, meaning a chicken's foot, in reference to the appearance of the leaves.

Locality: Waterloo Farm, Blue Layer (33° 19' 23.9"S 026° 32' 11.4"E) (Fig. 1).

Stratigraphic horizon: upper Witpoort Formation, Witteberg Group, South Africa.

Age: late Famennian.

Holotype: AM 7540 (Plate I, no. 3).

Additional material: AM 7541.

Diagnosis: Axes at least 29.5 cm long and 6–9 mm wide ($n = 2$), parallel-sided, with up to two isotomous dichotomies. Microphyllous leaves pseudowhorled, inserted in a low helix up to 20° from transverse, 8–12 leaves per turn of the axis, leaves alternating in successive pseudowhorls, which occur at intervals of 2.5–5 mm. Leaves with emergent, longitudinally elongate, swollen bases 1.5–4 mm high and 0.5–1.5 mm wide. Leaves persistent, elongate, slender, 17.5–21.9 mm long, trifurcating at around 5/6 of length, up to 0.9 mm wide prior to division, distal segments around 0.3 mm wide tapering to acute tips, median segment 3.3–3.9 mm long ($n = 3$), lateral segments 2.3–3 mm long ($n = 8$). Fertile parts unknown.

Colpodexylon mergae species nova:

Plate II, 1–4; Plate III, 1–5, Plate IV, 1–4, Plate V, 1–5

Etymology: mergae from Latin, meaning a hayfork, in reference to the appearance of the leaves.

Locality: Coombs Hill, Inner Outcrop (33° 17' 54.6"S 026 45' 40.2"E) (Fig. 1).

Stratigraphic horizon: (?) middle Witpoort Formation, Witteberg Group, South Africa.

Age: (?) mid Famennian.

Holotype: AM 7700 (Plate II, 1).

Paratype: AM 7701 a + b (Plate II, 2).

Additional material: AM 7702, AM 7703 a + b, AM 7704 a + b.

Diagnosis: Axes parallel sided, at least 31.6 cm long and 5–13 mm wide. Persistent leaves pseudowhorled, inserted in a low helix up to 20° from transverse, 10–12 leaves per turn of the axis, alternating in successive pseudowhorls. Successive pseudowhorls occur at intervals of 4–6 mm down to 2 mm apically. Leaves microphyllous with emergent longitudinally elongate swollen bases 2–3 mm high and up to 1 mm wide, microphylls diverging from the stem at 60–90°, elongate, slender, at least 23–31.9 mm long, trifurcating at 2/3 to 3/5 of total length, up to 0.8 mm wide prior to division, distal segments around 0.25 mm wide each tapering to an apparently acuminate tip, median segment longer than laterals, median segment 8.4–13.7 mm long ($n = 6$), lateral segments 7.5–8.9 mm long ($n = 8$). Fertile organs unknown.

4. Description of material

4.1. *Colpodexylon pullumpedes* species nova

4.1.1. Axes

The material ascribed to this species includes two slabs, each with a single specimen, both having leaves of a similar size and shape (Plate I, 1, 3). Axes are 15.1 cm and 29.5 cm in preserved length, the longer of them, AM 7541, exhibiting two dichotomies spaced 18.9 cm apart (Plate I, 1). Axes are 6–9 mm wide and are very regular in width. Following dichotomy, daughter branches are equal to each other and to the parent axis in width. Daughter branches diverge at angles of 35°–45°. The two dichotomies of specimen AM 7541 produce daughter branches which enter the rock matrix at different angles. At the first dichotomy the right daughter branch descends into the matrix beneath the bedding plane of parting. At the second dichotomy the left axis does so. Preparation of the right-hand branch of the first dichotomy suggests that it was truncated prior to burial.

4.1.2. Leaf distribution and morphology

Stems are covered by persistent leaves inserted in a low helix, at up to 20° from the transverse (Plate I, 2, 7). The low helical angle creates the impression that leaves are inserted in whorls, and their arrangement is termed pseudowhorled. Pseudowhorls are well spaced, occurring in intervals of 2.5–5 mm. Four to six leaf bases are visible in a row, suggesting 8–12 leaves per turn of the axis (Plate I, 7, 8).

The attachments of leaves to the axis are marked by false leaf scars, where leaves have been broken off at the base, remaining in the matrix of the counterpart. Leaf bases are swollen, 1.5–4 mm high and 0.5–1.5 mm wide and alternate in successive pseudowhorls. This base is elongated parallel to the stem, and in profile it protrudes from the stem margin, being deepest apically where it gives rise to a leaf. The emergent swollen leaf bases are most clearly seen on the holotype, AM 7540 (Plate I, 2). The distal region of AM 7541 shows leaf bases in face view, which are teardrop shaped with a rounded apical margin, tapering downwards to a point (Plate I, 8).

Four characteristic leaves, three of which remained visibly attached to stems, were exposed by *dégagement* (Plate I, 2, 7). These are consistent in size and morphology. Numerous incompletely exposed leaves attached to the holotype diverge from the stem, typically at angles of 30°–70° but up to and exceeding 90°. The complete leaf (excluding the swollen base) is 17.5–21.9 mm in length ($n = 4$). The leaf is narrow and elongate, trifurcating at around 5/6 of the total leaf length. It has very straight margins, widening slightly from the base up to the point of trifurcation, where it is maximum 0.7–0.9 mm wide. The three distal segments of the leaf are initially equal in width, around 0.3 mm wide,

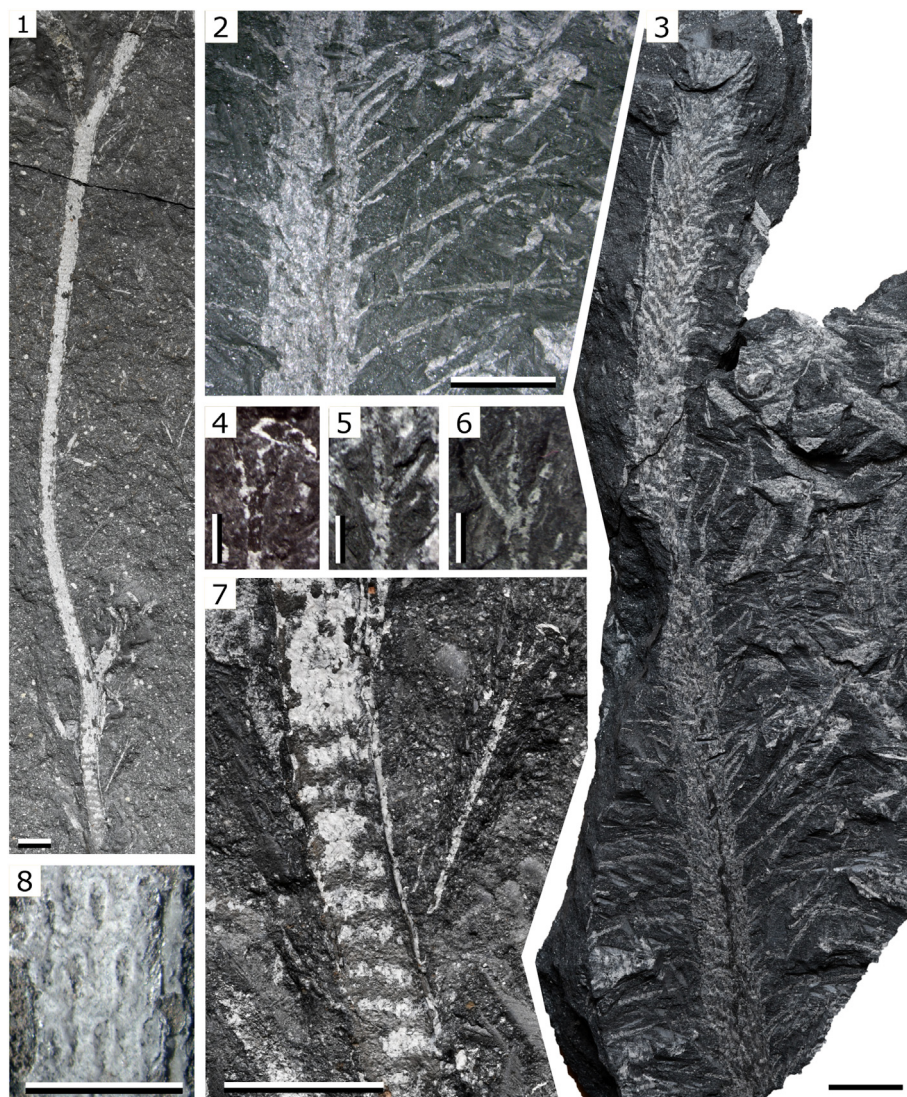


Plate I. *Colpodexylon pullumpedes* sp. nov. from Waterloo Farm; **1**) elongate axis showing two bifurcations (AM 7541a), **2**) enlargement from (3) showing the leaves, **3**) the holotype (AM 7540), **4**) enlargement from (1) showing a trifurcate leaf tip, **5**) and **6**) enlargements from (2) showing trifurcate leaf tips, **7**) enlargement from (1) showing the proximal axis with leaf, **8**) the distal axis of AM 7541a, showing leaf base morphology. All scale bars = 10 mm, except (4, 5, 6) which are 2 mm and (8) which is 5 mm.

each tapering to a point (Plate I, 4–6). The medial segment is the longest at 3.3–3.9 mm ($n = 3$), and the lateral ones are 2.3–3 mm long ($n = 8$). Lateral segments diverge from the medial one at 15°–40°.

No sporangia were observed on either of the specimens.

4.2. *Colpodexylon mergae* species nova

Five specimens from the Inner Outcrop horizon at Coombs Hill are attributed to *Colpodexylon mergae*. Four of these (Plate II, 1–3, Plate III) are portions of axes with diagnostic leaves attached, and the fifth (Plate II, 4) has incomplete leaves, but is attributed to the same species as it occurs at the same horizon as the others and is otherwise consistent with the diagnosis.

4.2.1. Axes

Axes are 5–13 mm wide and 48–316 mm long and are mostly very regular in width. None of the specimens are branched. The holotype, AM 7700, is a short segment of axis covered by leaves with swollen bases, which tapers slightly toward the tip. A congruent decrease in the spacing of leaf base pseudowhorls, suggests that the tip of the specimen represents the apex, or near apex, of the plant (Plate II, 1). Tentatively assuming that their full lengths are exposed, leaves on this

specimen are shorter than those of the other specimens (see Fig. 2 for comparison). AM 7704 a + b (Plate III, 1–5), the longest axis by far, tapers from 12 mm wide, to about 5 mm wide distally, before being truncated by the edge of the rock. The tapering of AM 7704 may also indicate proximity to an apex. All other axes are truncated at both ends by rock breakage or taphonomic damage. Axes are ornamented by leaf bases, but appear otherwise smooth, except for AM 7704, which presents, toward its apical part, a pattern of continuous sinuous grooves that meander longitudinally between the leaf bases. These latter are mounted on corresponding ridges.

4.2.2. Leaf distribution and morphology

Leaf bases are arranged in a low helix, inclined at up to 20° from a transverse plane (Plate IV). Each helical turn of the axis comprises 10–12 leaves, based on five or six consistently visible on one side of the axis. Leaf bases in successive pseudowhorls are not arranged in a vertical line, but alternate. Pseudowhorls occur at 4–6 mm intervals, with smaller intervals (down to 2 mm) measured from the compact area near to a putative growth tip (Plate II, 1).

Bases of leaves are variable in appearance: observed in face view, they range from swollen and elongate to circular or arched. The smaller, arched base is interpreted as representing a false leaf scar where the

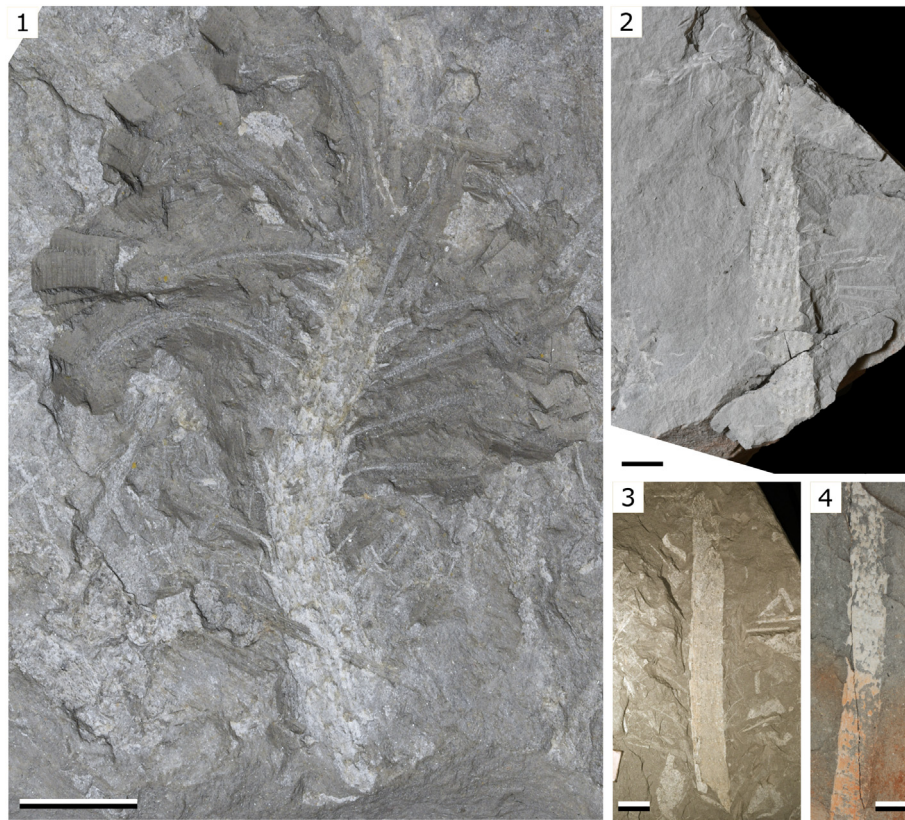


Plate II. *Colpodexylon mergae* sp. nov. from Coombs Hill; **1**) holotype of the species, (AM 7700), **2**) axis with typical leaves attached (AM 7701b), **3**) axis with taphonomically damaged leaves attached (AM 7702), and **4**) axis with incomplete leaves (AM 7703a). All scale bars = 10 mm. See [Plate V](#) for leaf enlargements.

parting plane of the matrix has intersected the leaf, with the remainder of the leaf remaining in the matrix of the counterpart. On the holotype, each leaf is attached to a swollen base of mineralized organic tissue 2–3 mm long by up to 1 mm wide, with its long axis parallel to the stem. In profile along stem margins of the specimen, leaf bases appear to emerge from the stem surface ([Plate IV](#), 1). Here, in sagittal view, they stand about 1 mm proud of the stem apically, and from there tapering proximally toward the stem. A narrow, elongate leaf emerges from the top of the swollen base. On other specimens the leaf bases are not as conspicuously swollen in profile.

The distal region of the axis on AM 7701 appears to be withered and reduced in girth, and is sharply bent to the side ([Plate II](#), 2). Here all that can be seen of the axis are the swollen leaf bases, from which well-preserved leaves emerge. One such leaf base and its corresponding leaf appears to have separated from the axis and occurs in isolation (Arrow on [Plate IV](#), 2).

False leaf scars visible in face view on AM 7703 are arched to circular structures around 1 mm high and wide ([Plate IV](#), 3). These are mounted on longitudinally elongate ridges which taper in a proximal direction from the apical false leaf scars, producing a roughly teardrop shaped structure. Proximally on AM 7704 the axis surface between similar false leaf scars appears smooth and flat ([Plate III](#), 4), but more distally the axis exhibits prominent ridges and grooves ([Plate III](#), 3). Here, the leaf bases occur on longitudinally elongate ridges, with sinuous grooves meandering between the bases. Leaf bases from opposing cortical surfaces are superimposed along this distal region of the axis; those of the underlying cortical surface appearing in negative relief. This superimposition occurs where the axis has not been filled internally by sediment.

Leaves emerge from the apex of the leaf base and diverge at 60–90° from the stem. Near the base of leaves, where they depart from the stem, the leaf appears to have a furrow along the midline, which may continue for up to half of its length ([Plate V](#), 1, 2). The leaf lamina is

narrow and elongate, trifurcating at 2/3 to 3/5 of its entire length ([Plate V](#), [Fig. 2](#)). Leaves are 23–31.9 mm long and up to maximum 0.7–0.8 mm wide prior to division. The widest point on the leaf usually occurs immediately prior to division. Trifurcation produces three distal segments of equal width (around 0.25 mm) which taper evenly to an acute tip ([Plate III](#), 5). It is uncertain whether the ultimate tips of leaves have been exposed during preparation as the segments distally taper to be so narrow as to preclude further dégradation. An acuminate tip is, however, suggested. In such circumstances, it is usually impossible to judge the full extent of leaf length, and recorded values are regarded as minima ([Berry et al., 2000](#)). The preserved length of lateral segments (7.5–8.9 mm) is less than that of medial segments (8.4–13.7 mm). The lateral segments diverge from the medial by up to 10°. Leaves are abaxially curved to straight, but can be sharply bent abaxially ([Plate V](#), 4) or adaxially ([Plate V](#), 5). Variations in leaf posture clearly result from taphonomic damage. Leaves preserved on bedding planes will generally have been twisted perpendicularly to their orientation *in vivo*, and this may have produced a straightening effect. Note damage to the proximal regions of leaves on AM 7701, evidencing that they have been twisted ([Plate V](#), 4). Leaves in attachment to the holotype occur in three-dimensional space within the matrix. Extending from the axis margins, they are preserved side-on, as they would have been orientated in life. A relatively quick burial is suggested by the specimen. From this evidence, abaxial reflexing of leaves as seen on the holotype, suggests their life posture ([Plate V](#), 1, 2, [Fig. 3](#)).

5. Discussion

5.1. Taphonomy

The preservation of plant tissue is subject to taphonomic variability in this South African material. An advanced degree of decay and remineralization has obliterated all cellular detail, so that interpretation

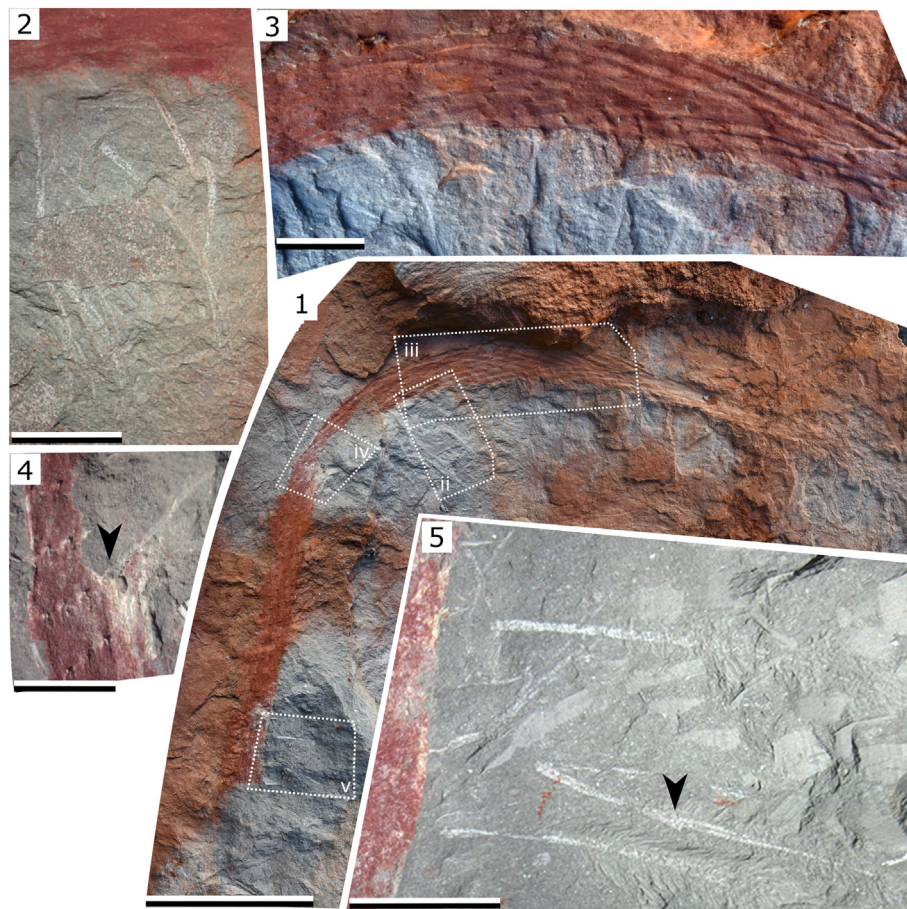


Plate III. *Colpodexylon mergae* sp. nov. from Coombs Hill **1**) AM 7704 (scale bar = 5 cm). **2–5**) Enlargements from (1), their positions on the specimen marked by stippled lines and indicated by roman numerals (scale bars for 2–5 = 10 mm). **2**) Numerous overlapping trifurcate leaves, some of them attached to axis. **3**) Pattern of grooves and ridges ornamenting the axis. **4**) Showing a leaf at top right ascending into the matrix overlying the axis, from its attachment to a leaf base (arrowed). **5**) Partial leaves adjacent to the axis, one of which shows clearly the point of division (arrowed) from which the middle segment tapers gradually to an acuminate tip.

of the original structures is tenuous and relies on evidence from studies on anatomically preserved material.

A pattern of meandering longitudinal ridges and furrows observed on *Colpodexylon* axes was initially interpreted as originating from superimposition of the characteristic lobed vascular strand during compression (Banks, 1944). Similar patterns observed on axes of other protolpidodendrolean genera, which bear 'ridged' rather than lobed xylem, are interpreted as arising from thickened cortical cells (Grierson and Banks, 1983). In light of this, a detailed taphonomic explanation was invoked for the preservation of originally thickened cortex as grooves in *Colpodexylon* axes (Berry and Edwards, 1995).

Such ridges and grooves are variably expressed on *C. mergae* axes, but not on the two *C. pullumpedes* specimens. The ridges, where seen, correspond to leaf bases, with sinuous grooves that meander longitudinally in between. The holotypes of both species lack this axis texture, but show structures of mineralized organic tissue at the bases of leaves. Swollen leaf bases of a similar size and shape were described from the type material of *Colpodexylon* by Banks (1944), who considered them to be submerged beneath the stem surface. Berry and Edwards (1995) considered swollen leaf bases in the type species to be taphonomic relicts, though 'short-tipped' *Colpodexylon* species are united by the presence emergent swollen leaf bases (Berry and Edwards, 1995). It is clear that both the South African long and short-tipped species exhibit swollen leaf bases, but how these structures are related to thickened areas of outer cortex is uncertain.

Leaf bases on the holotypes of both species visibly emerge from the surface of the axes. Swollen leaf bases may have had a higher

preservational potential than other axial tissues, as demonstrated by a paratype of *C. mergae* on which the distal part of the axis has withered, leaving behind a scatter of swollen bases with leaves attached. Although this might suggest the possibility that the apparently emergent leaf bases on the holotypes are the result of decay of the outer cortical tissues, the relatively intact nature of these two specimens, showing little evidence for preburial damage or decay counters the possibility. We therefore reconstruct the leaf bases as having primarily emerged from the surface of the axes in both species (Fig. 3).

5.2. Taxonomy

The possession of helically inserted leaves which trifurcate on a single plane indicate that the two species described here belong to the lycopsid Order Protolpidodendrales, genus *Colpodexylon* Banks, 1944, according to the revised generic diagnosis of Berry and Edwards (1995). *Colpodexylon* has previously been recorded from the Middle to early Late Devonian (Berry and Edwards, 1995; Berry et al., 2000; Gensel and Berry, 2001). Seven species recognized prior to this study (Table 1), include two from the Upper Eifelian to Lower Frasnian of New York (see Section 5.3 below), three from the Givetian or Lower Frasnian of Venezuela, and two from the Givetian of North and South China respectively. Material comparable to the younger New York species, *C. deatsii*, has also been reported from the (?) Lower Frasnian of Columbia (Berry et al., 2000). Equivocal reports of *Colpodexylon* include a stratigraphically poorly constrained example from Vietnam on which trifurcate leaves were not clearly demonstrated (Janvier et al., 1989),

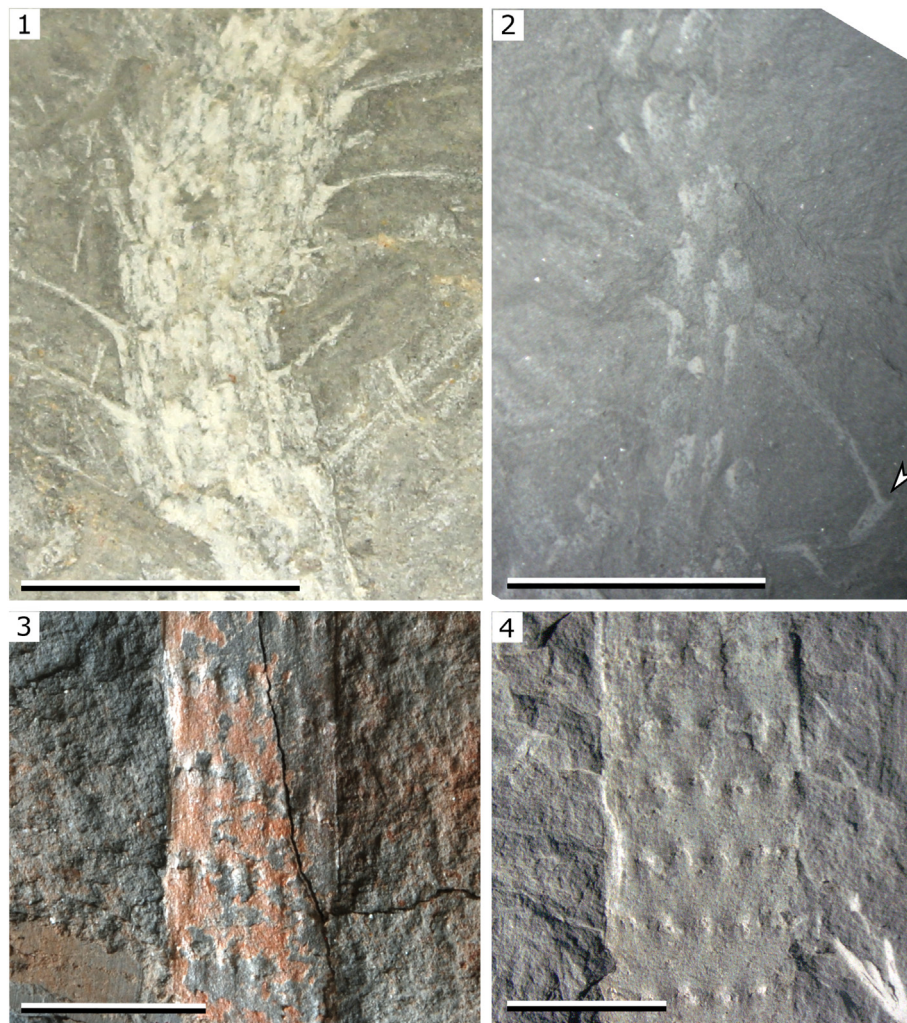


Plate IV. Variation in axis and leaf base morphology of *Colpodexylon mergae* sp. nov., showing enlargements of; **1**) the holotype, with emergent, swollen leaf bases (AM 7700), **2**) distal part of AM 7701b showing swollen leaf bases with leaves attached. Arrow indicates a leaf base which has been separated from its axis, **3**) close up of AM 7703a showing leaf bases as teardrop shaped ridges arranged in well-spaced pseudowhorls, under low-angled illumination from left, **4**) axis (AM 7701a) showing leaf bases under low-angled illumination from top left. All scale bars represent 10 mm.

and a species described from the Famennian of Ukraine, '*C. schopfii*' Lemoigne and Itschenko, 1980. Though the latter was tentatively assigned to *Colpodexylon*, Berry and Edwards (1995) challenged this assignment as the leaves were smaller than any known *Colpodexylon* species and were not proven to have been trifurcate. Furthermore, the given reconstruction of a leaf by Lemoigne and Itschenko (1980) shows the leaf to divide three-dimensionally, which is inconsistent with the revised generic diagnosis.

Species of *Colpodexylon* were informally characterized by Berry and Edwards (1995) as either long-tipped or short-tipped species. Long-tipped *Colpodexylon* have leaves which trifurcate at around half of the length of the leaf, whilst leaves of short-tipped species divide distally to produce proportionally short tips (Berry and Edwards, 1995). The two new species, recovered from separate localities, share a number of characteristics such as swollen leaf bases arranged in well-spaced pseudowhorls and a similar number of leaves per helical turn of the axis, which would make them difficult to distinguish on the basis of isolated axes. They are however clearly distinct in having long-tipped (*C. mergae*) and short-tipped (*C. pullumpedes*) leaves.

Colpodexylon mergae from Coombs Hill is very comparable in leaf morphology to the New York State long-tipped species, *C. deatsii* Banks, 1944, from the earliest Frasnian and *C. trifurcatum* Banks, 1944 from the early Middle Devonian. There is significant overlap in the

range of leaf sizes recorded in *C. mergae* and *C. deatsii*, although the former includes slightly longer leaves and has fewer leaves per turn of the axis (Table 1). *C. mergae* also has longer lateral segments relative to medial segments than *C. deatsii*. Like *C. mergae*, *C. trifurcatum* has a lower number of leaves per turn of the axis than *C. deatsii* (Table 1). *C. mergae*, however, differs from both *C. deatsii* and *C. trifurcatum* in exhibiting a greater degree of spacing between successive pseudowhorls and between leaf bases, which usually do not contact one another. The well-spaced leaf bases are similar to those of *C. coloradense* Berry and Edwards, 1995, a Venezuelan short-tipped species, but leaves of the latter are far smaller. Though the leaves of *C. mergae* are similar to those of *C. deatsii* they differ in leaf proportions and in their pattern of distribution on the axis.

Colpodexylon pullumpedes has planate leaves up to 22 mm in length that divide distally at around 5/6 of their length to produce proportionally short tips. This distinguishes it from *C. mergae* and likewise from the two New York species. Described short-tipped species of *Colpodexylon* include one from Venezuela, *C. coloradense* Berry and Edwards, 1995, and three from China, the validity of which have been disputed. Two of these, *C. gracilentum* Dou and Sun, 1983 emend. Xu and Wang, 2011 and *C. laminatum* Dou and Sun, 1983 from NW China have been synonymized (Xu and Wang, 2011). Prior to this their assignment to *Colpodexylon* had been challenged and suggestion made that

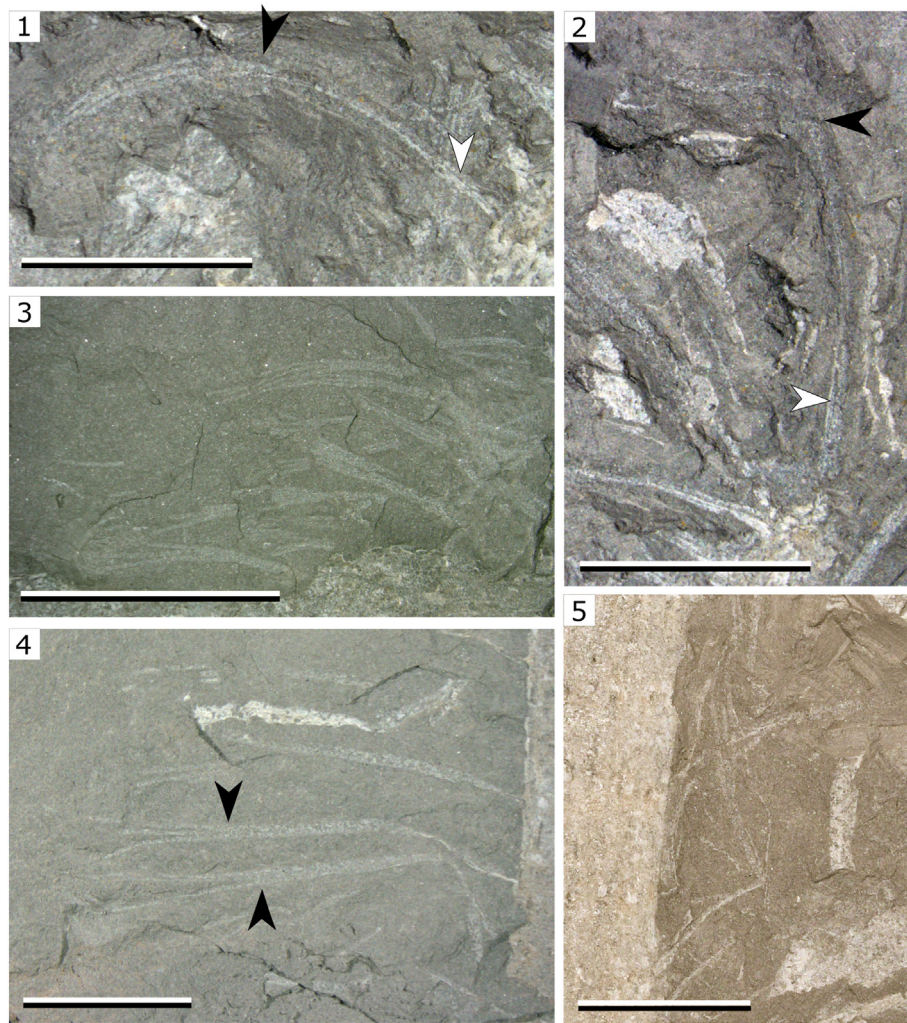


Plate V. Leaves of *Colpodexylon mergae* sp. nov.; **1** and **2**) enlargement of leaves from AM 7700 (Plate II, no. 1), **3**) enlargement of several overlapping leaves on AM 7701b (Plate II, no. 3), **4**) leaves attached to axis of AM 7701a, **5**) enlargement of a leaf from AM 7702 (Plate II, no. 2). Black arrows on 1 and 4 indicate estimated point of trifurcation, and white arrows on 1 and 2 indicate a medial furrow on the proximal region of the leaf. All scale bars = 10 mm.

preparation of the leaves might reveal them to be more similar to *Leclercqia* or perhaps *Minarodendron* (Berry and Edwards, 1995). Inclusion of the remaining Chinese species, *C. variable* Schweitzer and Cai 1987 emend. Ma and Xu, 2017 from Southern China within *Colpodexylon* has also been challenged on the basis that this species lacks a characteristic lobed xylem strand (Wang and Berry pers. comm. in Xu et al., 2018). Devonian lycopod species with three-tipped leaves described from China also include *Minarodendron* (Schweitzer and Cai) Li 1990 and *Tiamophyton* Xu et al., 2018. The former has leaves which trifurcate three-dimensionally, distinguishing it from *Colpodexylon* (Liu et al., 2013). *Tiamophyton* has small three-tipped leaves bearing an abaxial keel (Xu et al., 2018). We note that all Chinese protolpidodendraleans with trifurcate leaves have leaves less than 10 mm in length. With their proportionally short leaf tips, the leaves of *C. pullumpedes* most closely resemble *C. coloradense* from Venezuela though they too were much shorter than those of *C. pullumpedes* (5–8.7 mm as opposed to 17.5–22 mm long).

Colpodexylon mergae and *C. pullumpedes* resemble ‘short-tipped *Colpodexylon*’ in having emergent swollen leaf bases, but both present leaf lengths overlapping with the overall ranges reported for the long-tipped group, and share a number of leaves per pseudowhorl that is intermediate between the lower number generally suggested for short-tipped variety and the higher number proposed for the long-tipped

variety (see Table 1 for comparison). Overall, the two species present a suite of characters intermediate between the known species of *Colpodexylon*, confirming the prediction of Berry and Edwards (1995) that intermediaries would be found with further searching. As *C. pullumpedes* and *C. mergae* differ principally in the length of their leaf tips a sister-species relationship is not excluded.

5.3. Range of the genus

Occurrences of *Colpodexylon* in New York, according to Banks (1944), suggest a stratigraphic range of lower Middle to lower Upper Devonian for the genus. This range probably encompasses the ages of material from Venezuela and Columbia, although the latter two occurrences are to some extent dated on the basis of floral comparisons to New York (Berry and Edwards, 1995; Berry et al., 2000). Berry and Edwards (1995) considered the genus to range from late Eifelian to early Frasnian, a period of less than 10 million years (Cohen et al., 2013). Prior to the present study, the stratigraphically uppermost occurrence of the genus was the type locality of *C. deatsii*; locality 1 of Banks (1944), which he reported as occurring at a quarry along the Delaware River, about one mile southeast of Pond Eddy, New York. Banks included the locality within the Delaware River Flats, considering it to fall within the lower Upper Devonian. The locality, according to C. A. Ver Straeten

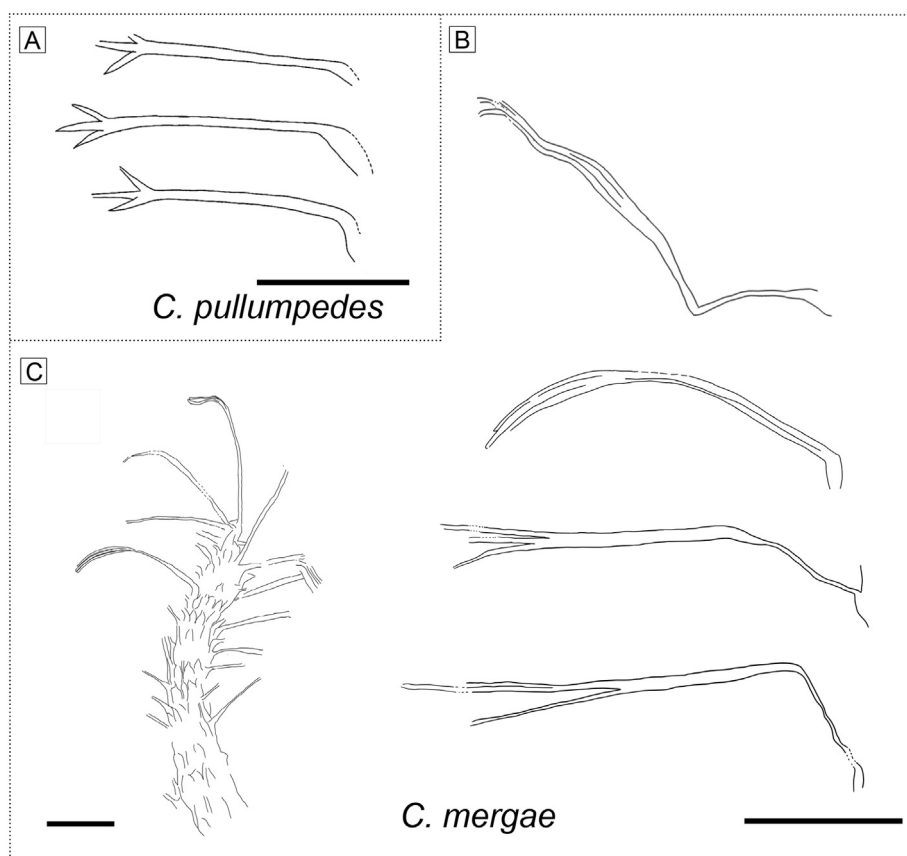


Fig. 2. A) Line drawings of leaves of *Colpodexylon pullumpedes* sp. nov., specimen AM 7540, inverted from original orientation. B) Line drawings of leaves of *Colpodexylon mergae* sp. nov., the lower two from AM 7701, the upper from AM 7702 (inverted), and the remaining leaf from AM 7700. C) Line drawing of the holotype of *C. mergae* (AM 7700). Stippled lines are interpretive on all drawings, all scale bars = 10 mm.

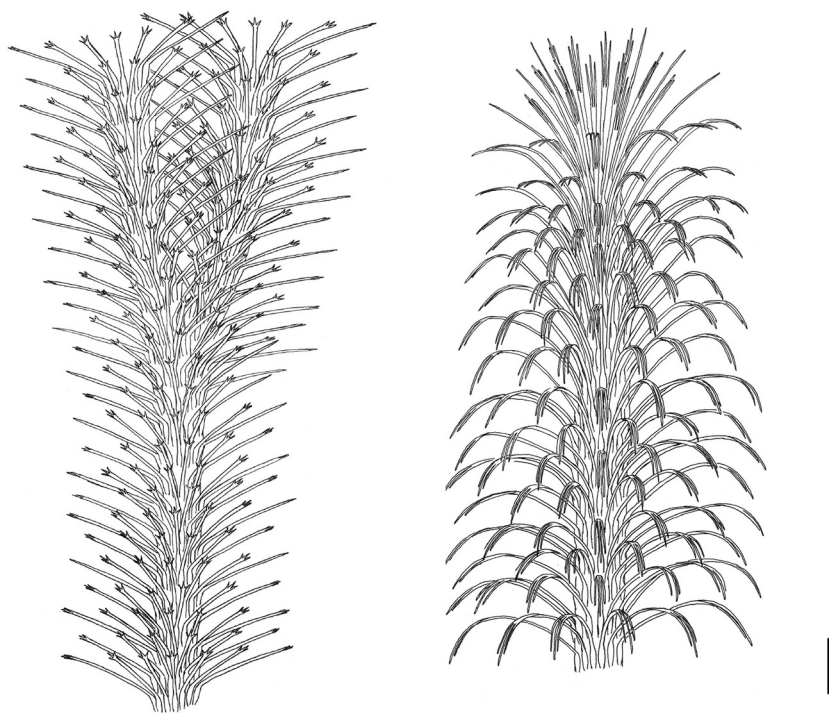


Fig. 3. Suggested reconstructions of *Colpodexylon pullumpedes* sp. nov. (left) and *Colpodexylon mergae* sp. nov. (right). Scale bar represents 10 mm.

Table 1
Table of characters for *Colpodexylon* species, modified from [Berry and Edwards \(1995\)](#). ?taph. = taphonomic relicts?

Species	Stem width (mm)	Swollen leaf base (mm)	Leaves/Pseudo-whorl	Length X Width (mm)	Central segment (mm)	Lateral segments (mm)	Sporangia (mm)	Authors	Age and palaeolatitude
<i>C. deatsii</i>	12–15	?taph. 3.5 X 1	16–20	20–30 X 0.5–0.8	12–15	4–8	1.8–3.8 X 0.5–1.6	Banks (1944) , Grierson and Banks (1963)	Early Frasnian, sub-tropical
<i>C. trifurcatum</i>	10–25	?taph. 3–4 X 2	8–12	15–30 X 1.4–2	7.5–15	3–5	4.3–6 X 1.5–2.8	Banks (1944)	Late Eifelian, sub-tropical
<i>C. cachiriense</i>	5.3–9.5	–	7–9	~ 14.7 X 0.6–1	+–7	+–3	–	Edwards and Benedetto (1985)	Givetian/Frasnian sub-tropical
<i>C. camptophyllum</i>	12–30	–	16–20	18–19 X 0.6–1.2	3.3–8.6	1.4–3.5	2.4–4.3 X 0.8–1.8	Berry and Edwards (1995)	Givetian/Frasnian sub-tropical
<i>C. coloradense</i>	10–20	–	5–8	5–8.7 X 0.9–1.9	1.2–2.0	0.5–1.6	2.4–4.3 X 0.8–1.6	Berry and Edwards (1995)	Givetian/Frasnian sub-tropical
? <i>C. variable</i>	14–18	1.3–1.7 X 0.8–1.5	15–16	5.3–7.7 X 0.4–0.7	2.0–2.5	0.9–1.1	1.1–1.2 X 1.0	Schweitzer and Cai (1987) , Ma and Xu (2017)	Givetian, equatorial
<i>C. gracilentum</i>	3.3–15	1.5–2 X 0.5–0.7	7–8	6.5–7.8 X 0.9–1	1.5–2.1	1.5–2.1	2.9–3 X 2–2.2	Dou and Sun (1983) , Xu and Wang (2011)	Givetian, equatorial
<i>C. mergae</i> sp. nov.	6–13	2–3 X 1	10–12	23–31.9 X 0.7–0.8	8.4–13.7	7.5–8.9	–	This study	Famennian, sub-polar
<i>C. pullumpedes</i> sp. nov.	6–9	2–4 X 0.5–1.5	8–12	17.5–22 X 0.7–0.9	3.3–3.9	2.3–3	–	This study	Famennian, sub-polar

(pers. comm. 2019) has more recently been mapped within the upper part of the Oneonta Formation (= middle Delaware River Formation of [Rickard, L. V., \(1975\)](#)) supporting a probable Lower Frasnian age, as suggested by [Banks \(1944\)](#). Hence, previous evidence suggested the last appearance of *Colpodexylon* to be around 380 Ma.

5.4. Palaeogeography

Material herein diagnosed not only represents the first unequivocal record of *Colpodexylon* in southern Gondwana but also its first known record from the Famennian. These younger occurrences

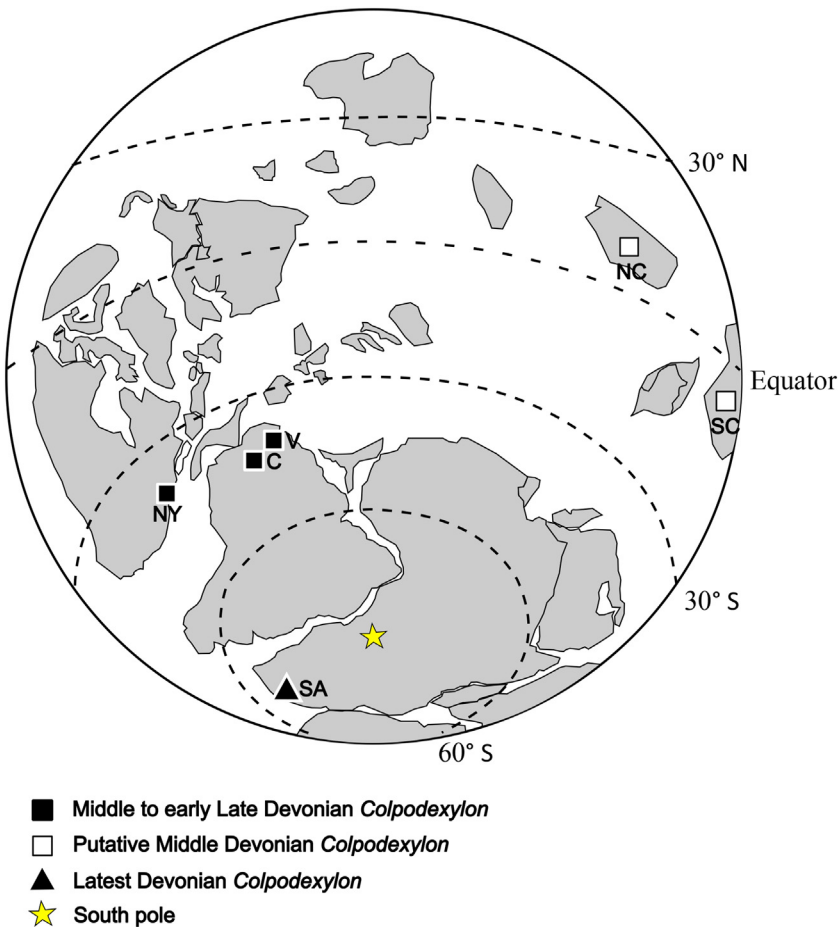


Fig. 4. Palaeogeographic map of the Late Devonian (370 Ma), based on [Torsvik and Cocks \(2004\)](#), showing occurrences of *Colpodexylon* in New York (NY) ([Banks, 1944](#)), Venezuela (V) ([Berry and Edwards, 1995](#)), Colombia (C) ([Berry et al., 2000](#)), North China (NC) ([Xu and Wang, 2011](#)), South China (SC) ([Ma and Xu, 2017](#)) and South Africa (SA) (this work).

extend the range of the genus by between 10 and 20 million years (Cohen et al., 2013).

Notably, according to the palaeogeographic reconstruction of Torsvik and Cocks (2004) (Fig. 4), *Colpodexylon* occurrences from New York, Venezuela and Colombia occurred within a band, just south of the southern tropic parallel, with putative Chinese species having been reported from the palaeotropics. These palaeolatitudes remained largely unchanged from the Middle to Late Devonian (Scotese and Barrett, 1990; Torsvik and Cocks, 2013; Domeier and Torsvik, 2014). By contrast, the South African examples occurred substantially farther south, at greater than 60 degrees of latitude.

It has been suggested that high-latitude environments may have acted as refugia for primitive plants during the Late Devonian and Early Carboniferous (Prestianni et al., 2015). This is evidenced by Devonian-like plant communities in the Tournaisian of Argentina, including the genus '*Haplostigma*' (Prestianni et al., 2015). Despite being excluded from tropical to subtropical regions by the Famennian, protilepidodendrolean lycopods persisted in colder, high-latitude environments, exemplified by the Witpoort Formation, until at least the late Famennian, and likely beyond the end of the Devonian Period. The South African occurrences therefore suggest a Late Devonian high latitude refugium for Middle Devonian *Colpodexylon*.

It is currently uncertain whether *Colpodexylon* is represented among Middle Devonian protilepidodendrolean lycopods from the Bokkeveld Group of South Africa which reportedly include '*Haplostigma*' (Plumstead, 1967; Penn-Clarke et al., 2019). It is therefore impossible at this stage to ascertain whether, like *Haskinsia*, *Colpodexylon* had an extensive latitudinal distribution during the Middle Devonian. Since the present occurrence is not contemporary with other occurrences, it is equally parsimonious to suggest that *Colpodexylon* habitats shifted from low to high latitudes during the Late Devonian.

6. Conclusions

In the genus *Colpodexylon*'s first confirmed record from high palaeolatitude strata, two new species are here described. They provide evidence of congeneric, but clearly distinct species from two localities. The Waterloo Farm species (*Colpodexylon pullumpedes*) is compared to short-tipped *Colpodexylon* species, with which it is similar in having proportionately short leaf tips. Its leaves are, however, more than double the length of any previously known short-tipped species. Aside from lengths of the leaf tips, it bears an overall similarity to the Coombs Hill derived *C. mergae*, in terms of leaf base morphology and arrangement, and the size of leaves prior to trifurcation. This latter species is comparable to the long-tipped *Colpodexylon* species, including the type species *C. deatsii* from the Lower Frasnian of New York State, to which its leaves are most similar. It is distinguished from *C. deatsii* on the basis of slightly longer leaves, with differing proportions in length of leaf tips, as well as fewer leaves per pseudowhorl.

These new species of *Colpodexylon* extend both the geographic and temporal ranges of *Colpodexylon*. It is shown that the genus persisted in high-latitude environments until the late Famennian, more than 10 million years younger than previously known records. It is therefore hypothesized that southern Gondwana gave refuge to the genus toward the end of the Devonian Period.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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