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Enigmatic fossil plants with three-dimensional, arborescent-growth architecture from the earliest Carboniferous of New-Brunswick, Canada

Enigmatic, as well as uncertain, is the new Early Carboniferous fossil recorded by **Gastaldo *et al*.** (2024), which is interpreted to have been an understory tree from New Brunswick, Canada. The fossil evidence that, according to the reconstruction made using allometric equations (**Niklas**, 1994), would be an arboreal element with monopodial growth of about 3 m in height. The lower stem is covered by scars resulting from the detachment of the leaves, which are still attached towards the apex of the trunk, where there are approximately 200 of them with a spiral distribution. These partial leaves are 1.75 m long and do not follow the Fibonacci series (1/13 phyllotaxis). Although the evidence is fragmentary, they would appear to have branched three times.

The new fossil was named *Sanfordiacaulis densifolia* and due to the lack of morphological, anatomical, and reproductive evidence it has not been included in a suprageneric taxonomic category. **Gastaldo *et al.*** (2024) only make comparisons based on the preserved morphology and relate it mainly to Ferns and Pteridosperms. The general pattern of monopodial growth and leaf scars along the stem, with concentration of leaves or branches towards the apex, was common in the Lower Carboniferous in Lycopodophytae (**Orlova *et al.,*** 2017) and in other past and present groups. But, the available evidence makes it very difficult to place the tree in any definite lineage.

The reinterpretation of fossil evidence from fragments alone to propose new species, or even genera, has led to the proposal that rather than new taxonomic entities, many may have been different stages of development of the same species. As **Gastaldo *et al.*** (2024) point out, a fossil represents only the ontogenetic stage of the organism in the period of time when it was preserved. Evidence of the base of the tree is lacking, and what would be

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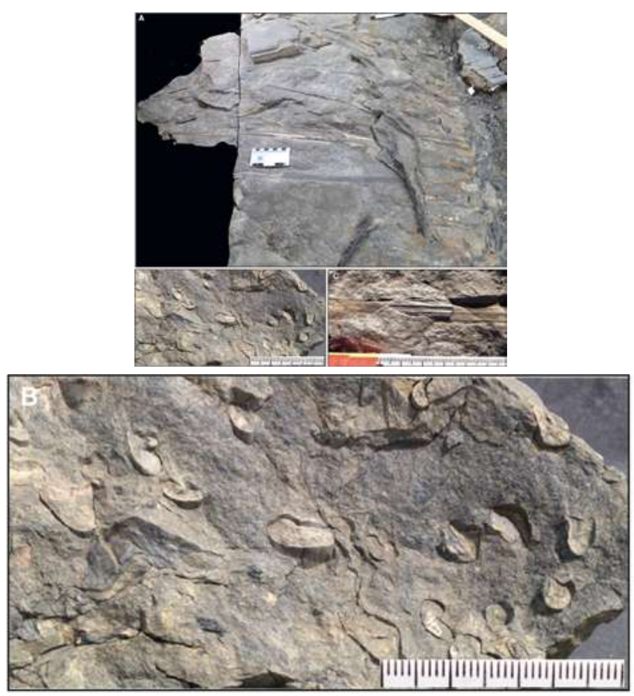
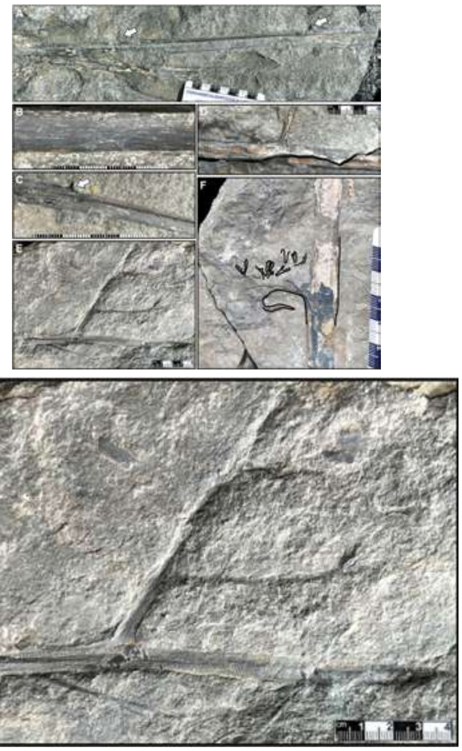
a 3 m individual could be one of greater height, like many from the Lower Carboniferous, a period when, according to **Gastaldo *et al.*** (2024), there were canopy trees or herbs, but no evidence for trees in the understory.

The base of the stem has not yet been found, a key to place it perhaps within Marattiales, Cyatheales, or Pteridosperms (**Gastaldo *et al*.,** 2024), because these groups developed abundant roots and root mantles in this part of the main axis (**Stewart & Rothwell,** 1993). This new fossil may not be in the evolutionary line of tree ferns, because **Ramírez** (2024) recently found that Cyatheales started their evolutionary history in the Triassic, almost 100 million years after the existence of *S. densifolia*. The anatomy of the petiole could give clues about its possible relationship with the Maratheales. In both Psaronius and some filicalean ferns the vascular tissue is “C” shaped, which also occurs in some Pteridosperms (**Stewart & Rothwell,** 1993). In extant ferns it has been seen that grooved petioles can present this shape mimicking the conductive tissue, which could be present in *S. densifolia*, considering that it has similar shaped petioles. In their **figure 4B Gastaldo *et al***. (2024) show petioles in transverse section; however, the vascular system is not preserved, and the interior of the petioles are mud filled.

Apparently, the leaves of *S. densifolius* are represented by branched axes up to a third order and the laminar pinnae or pinnules are not preserved. **Gastaldo *et al.*** (2024) point out that the leaf petioles were not dichotomous. However, in the lower part of **figure 5E** a dichotomous branching that is interpreted as photosynthetic laminae is presented. In that same figure, a second order branch appears, which could have developed by overgrowth, giving the appearance of a main structure with lateral branches.



"Figure 4. Trunk and petiolar features. Trunk and basal parts of leaves (right; NBM 22403/1) with adjacent block showing their continuation, indicating that leaves were longer than shown on main block. The counterpart removed and sectioned in figure 2D originates from the upper right (NBM 22403/2). Scale in cm and inches. NBM 22403-3. **(B) Petiole cross-sections proximal to the trunk exhibiting a heart-shaped geometry with an adaxial depression appearing as a longitudinal furrow in compressions. Scale in mm. NBM 23142**. (C) Mudcast petiole proximal to the trunk showing adaxial groove and fine striations. NBM 22403/2. Scale in cm and mm". (With permission of R. Gastaldo)



"Figure 5. Evidence of compound leaves and pinnules. NBM 22403/. (A) Portions of two leaves in close spatial proximity. Arrows indicate bases of second-order laterals departing from upper axis. Scale in cm and mm. (B) Petiole/rachis detail showing fine striations and adaxial groove (top). Scale in mm. (C) Leaf rachis with white arrow indicating departure of another lateral. Scale in mm. (D) Longer second-order lateral departing from rachis. Scale in cm and mm. **(E) Isolated rachis on large block with second- and third-order laterals. Scale in cm and mm**. (F) Rachis with poorly preserved, Sphenopteridiumlike, pinnules (black outline) departing from secondorder axes. Scale in cm and mm". (With permission of R. Gastaldo).

The Trimerophytopsida, Progymnosperms, and Pteridosperms exhibit a great morphological diversity in leaf structures to capture light. These features provided for better mechanical support and in the dispersion of reproductive structures (Niklas, 1997). It has been proposed that overgrowth and reduction alter the dichotomous branching of the earliest vascular plants (**Stewart & Rothwell,** 1993; **Niklas,** 1997). These foliar characteristics, in addition to the arborescent habit, could lead one to think that *S. densifolius* could be related to the Progymnosperms and, perhaps within these, to the Aneurophytales (**Stewart & Rothwell,** 1993). It is also possible that the plant could belong to the Pteridosperms. However, most of the fossils of the latter group show laminar structures and the petioles fork into two equivalent halves, each bearing photosynthetic laminae (**Stewart & Rothwell,** 1993). Nevertheless, the assignment and inclusion of *S. densifolius* into any of these groups will not be possible without a description of the anatomical and reproductive characteristics which, to date, have not been encountered.

The new fossil does not present “juvenile leaves” and, therefore, their departure from the growing tip is not known. If the developmental pattern was present, a possible relationship with the Marattiales, Progymnosperms, or Pteridosperms, in which a circinate vernation, typical of present-day ferns, may be concluded (**Tryon & Tryon,** 1982). Circinate vernation is a character recorded since the Paleozoic in the tree fern genus *Psaronius* (**Stewart & Rothwell,** 1993).

Another striking feature of *S. densifolia* is that leaf phyllotaxis does not follow the Fibonacci series, which is not unexpected considering that other fossil plants have been found that do not follow the pattern (**Turner *et al.*,** 2023). Phyllotaxis is the result of a physiological, genetic, and environmental adaptation interaction (**Niklas,** 1988), as auxin activity largely determines how the distribution of lateral organs will develop (**Niklas,** 1988; **Gola & Banasiak**, 2016). The formation of laterals, though, has been documented to change throughout the life of a plant in some taxa (**Guzman *et al.*,** 2022). A better understanding of these factors and their relationship in the evolution of land plants would help us understand the lack of this general pattern of lateral organ organization in some groups in the geological past. The Fibonacci series is present in all vascular plant groups; however, it is commonly absent in the Lycopodiales and in one of a closely related fossil group, the Drepanophytales (i.e., *Asteroxylon mackiei*; **Turner *et al*.,** 2023). Considering that the Pteridosperms and even some Upper Carboniferous ferns display this pattern of organization (**Stewart & Rothwell,** 1993), the taxonomic placement of *S. densifolia* becomes more confusing. Therefore, we will have to wait for new fossil finds of this plant to understand and interpret its relationships with the groups that developed during the early Carboniferous

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Editors´note

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