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## Title

Evolution: New fossil evidence for the diversification of angiosperm rooting systems in the Early Cretaceous

## Abstract

A monocot from the Early Cretaceous developed a cluster of anatomically similar roots from the base of stocky stem. This discovery indicates that angiosperm rooting systems were more diverse than previously thought at this time.

## Main Text

Most fossils of angiosperm roots from the Early Cretaceous that have been described to date are termed adventitious and developed from horizontal shoot axes called rhizomes [1–8] (Fig. 1). Rhizomes of many extant herbaceous plants grow horizontally through the surface of soil and develop roots that supply water and nutrients as well as tethering the axis to its growth substrate [9]. Leaves, vertically growing (orthotropic) shoots and often roots develop along rhizomes forming ramifying branched systems. The prevalence of this bauplan – root-bearing rhizomes – in the Early Cretaceous fossil record supports the hypothesis that early angiosperms developed a rhizotamous habit [10]. The recent paper by Coiffard *et al.*, 2019 [11] described a new Early Cretaceous monocot species *Cratolirion bognerianum* revealing that there was at least another type of rooting system present in the Early Cretaceous. The description of the fossil *Cratolirion bognerianum* demonstrates that another root type was in existence in the late Aptian to early Albian just over 100 million years ago [11].

*C. bognerianum* (Figure 1, 2A) develops a rosette of leaves from a stocky stem with roots developing from the lower portion of the stem. The roots are classified as adventitious because they develop from the base of the stem (Figure 1B). These adventitious roots form a cluster, and this type of root system where roots initiate from a local point in bundles are

classified as fascicular (*fasciculus* is the Latin word for bundle) (Figure 2B) [11]. Only one type of root developed from these fascicles in *C. bognerianum*; roots are the same diameter where they attach to the base of the stem and with similar branching architectures (Figure 2B). Fasciculate rooting systems of this structure were assigned as Type VII of Cannon's [12] rooting system scheme and characterises the roots of many extant monocots today such as the rooting system of *Oryza sativa* (rice) [13] (Figure 2C, D). *C. bognerianum* represents to our knowledge the earliest example of this type of rooting system preserved in angiosperms.

The discovery that *C. bognerianum* developed a Type VII root system is important because this system has not been described in other Early Cretaceous angiosperms that developed a rhizotamous habit with adventitious roots (Fig. 1). Furthermore, since *C. bognerianum* is one of the oldest crown group monocots it suggests that this type of rooting system may have been an evolutionary innovation of the monocots and therefore a synapomorphy of the group [11]. Although an interesting hypothesis, further work on this character is necessary as the development of fasciculate roots has not been surveyed extensively in extant angiosperms. Regardless of whether a fasciculate root system is a synapomorphy of crown group monocots, the discovery of *C. bognerianum* suggests that the earliest time this type of rooting system is found is within the monocots and adds a new type of rooting system to our understanding of early angiosperms.

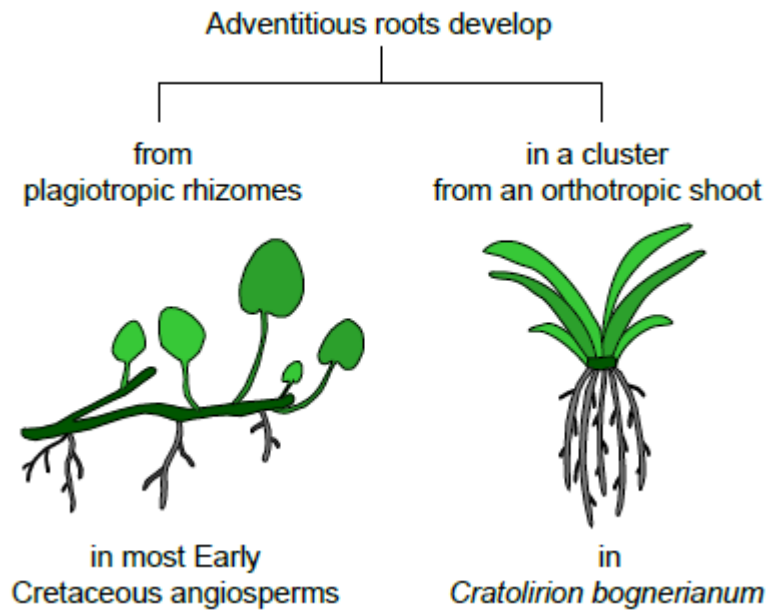
Within the bigger picture of angiosperm root evolution it also tells us, albeit from a small sample size, that the roots developed in these early angiosperms only account for a small subset of the types of roots that characterise living angiosperms. The roots of living angiosperms were divided into ten major categories by Cannon [12]. Adventitious roots developing from horizontal rhizomes only account for two of these root types (Type IX and X of Cannon [12]). This means that it is currently unknown when angiosperms evolved the other 8 rooting system types. The discovery that fasciculate roots (Type VII [12]) existed in early crown group monocots indicates that a rooting system of this type had evolved by the Early Cretaceous [11] and it begs the question, how many more extant rooting systems had evolved by this time.

Rooting systems have been largely overlooked in the debate on angiosperm origins – Darwin's abominable mystery. Understanding the evolution of angiosperm rooting systems has a key part to play in reconstructing the growth habits, symbioses, ecology and physiology of early angiosperms. These are all essential characteristics for reconstructing the evolutionary steps that led to the remarkable success of extant angiosperms. Furthermore, describing root evolution in early angiosperms is an essential starting place for understanding the rich diversity of angiosperm rooting systems alive today.

The discovery of *C. bognerianum* [11], a crown group monocot from the Early Cretaceous, represents a step forward in our understanding of rooting system evolution. *C. bognerianum* is the earliest species to be preserved with a fasciculate rooting system that differs in both its structure to the rhizotamous growth habit of many other Early Cretaceous angiosperms. It therefore represents a key fossil discovery for investigating rooting system evolution, and rooting character homologies at the base of the angiosperms.

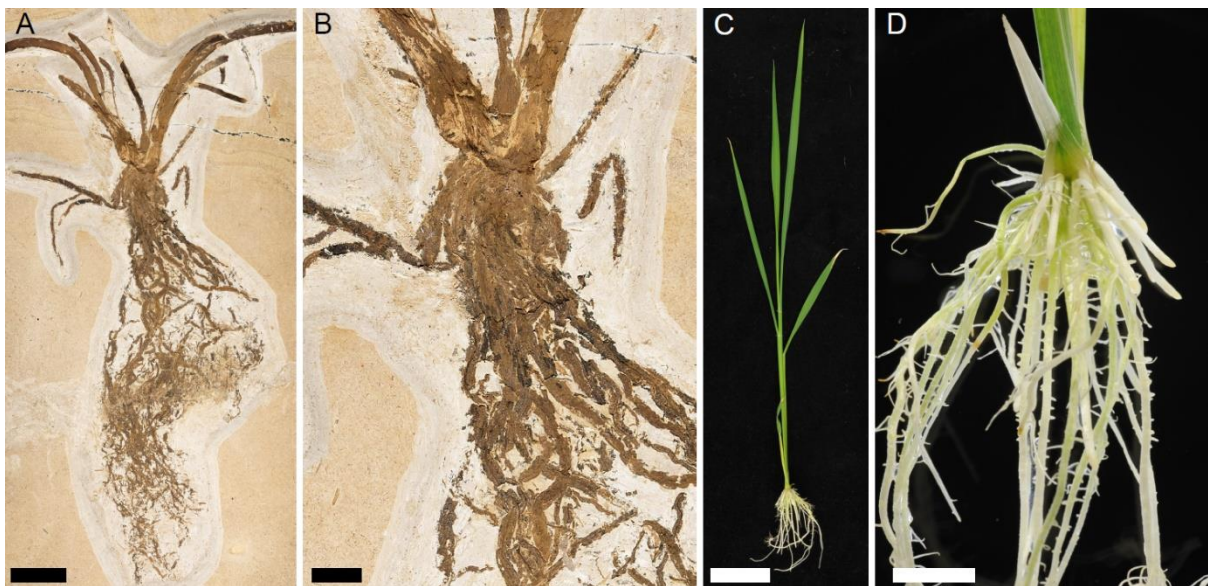
## Figure 1. Rooting system diversity in Early Cretaceous angiosperms.

Adventitious roots develop from plagiotropic rhizomes in most Early Cretaceous angiosperms but develop as a cluster at the base of an orthotropic shoot in the Early Cretaceous monocot *Cratolirion bognerianum*. Dark green, shoot system and rhizome; light green, leaves; grey, roots.



**Figure 2. The fasciculate root systems of extant and extinct monocots.**

(A, B) Paratype MB.Pb. 2002/854 of *Cratolirion bognerianum* [11]. The rooting system is described as fasciculate as a cluster of anatomically similar roots develop from the base of stem. (C, D) Many extant monocots including *Oryza sativa* (rice) develop similar fasciculate root systems. Scale bars, A, C, 2 cm, D, 2 cm, B, 1 cm. (A, B) reproduced with permission of Hwa Ja Götz and Clément Coiffard. (C, D) photographs courtesy of Thomas Hughes and John Baker.



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