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Age and identity of the oldest pine fossils

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In their study of charred conifer twigs from the Lower Cretaceous Chaswood Formation of Canada, Falcon-Lang et al. (2016) established the species *Pinus mundayi* that they interpreted as a "two needled" pine and the oldest stratigraphic evidence for the extant genus *Pinus*. This is based on their interpretation of what they thought was distinctive wood anatomy and paired needle bases of *Pinus* evident in their fossils, while the Valanginian age (ca. 140–133 Ma) is based on revised palynostratigraphy. If correctly interpreted, this material predates the oldest known species *Pinus yorkshirensis* from the Hauterivian–Barremian transition at ca. 131–129 Ma (Ryberg et al., 2012), and pushes back the earliest occurrence of the genus by 4–11 m.y. However, we consider that a more thorough examination reveals that *P. mundayi* is from the Valanginian–Barremian (ca. 140–125 Ma) and that Falcon-Lang et al. have misinterpreted the anatomy of their fossils and erroneously assigned them to the genus *Pinus*.

The Chaswood Formation palynoflora is dominated by pteridophyte spores including *Aequitriradites verrucosus*, *Distaltriangulisporites perplexus*, and *Trilobosporites canadensis*. Falcon-Lang et al. interpreted this to indicate an Early Cretaceous (Valanginian–Hauterivian) age based on North American studies such as Burden and Hills (1989), and based on the range top of *T. canadensis*, they considered it could be refined to early Valanginian following Taugourdeau-Lantz (1988). However, *T. canadensis* ranges from Tithonian to Barremian in North America (Pocock 1962; Burden and Hills 1989) while its range top in eastern Canada was cited as Hauterivian (Falcon-Lang et al., 2007). In Europe, this range top is early Albian (Herngreen, 1971); hence, significantly younger. Moreover, *A. verrucosus* and *D. perplexus* have ranges of Berriasian–Albian and Valanginian–Albian, respectively, in North America (Burden and Hills 1989). Hence, the spore association of Falcon-Lang et al. is Valanginian to Barremian in age (Burden and Hills 1989). Therefore, the early Valanginian age invoked by Falcon-Lang et al. for this material appears to be unreliable.

The "short shoot bases" with paired vascular bundles illustrated by Falcon-Lang et al. for '*P.*' *mundayi* were structurally misinterpreted and actually represent axillary branch scars as they appear at the periphery of the wood. Such branch traces are characteristic for all seed plants with axillary branching (Rothwell, 1976) where branch vasculature arises by divisions of two cauline bundles of the stele. Within conifers, this configuration characterizes short shoot branches of all types, including the five-needled pine, *P. arnoldii* (Klymiuk et al., 2011), revealing that branch traces alone do not identify the type of branch that they represent.

Although axial resin ducts with thin-walled epithelial cells in the wood of '*P.*' *mundayi* also occur in *Pinus* (Richter et al., 2004; Falcon-Lang et al. 2016), thin-walled epithelial cells occasionally occur in *Picea*, *Larix*, and *Pseudotsuga*. The cross-field pitting was interpreted to be fenestriform or pinoid (see the Supplementary Information) but similarity in pit appearance suggests that these could be taphonomic artefact. Crucially, their sample lacks ray tracheids, a feature diagnostic of all present-day *Pinus*. Likewise, the helically arranged short-shoot traces passing through the growth rings of '*P.*' *mundayi* are not diagnostic for two separate needle bases or for the genus *Pinus*. The characteristics of '*P.*' *mundayi* more closely conform to the genus *Protopinuxylon* Ekhold, which lacks ray tracheids, to which the species should be transferred.

Even if the wood anatomy described by Falcon-Lang et al. were diagnostic of extant *Pinus*, which the lack of ray tracheids argues against, there is no way of knowing when that combination of characters evolved. Was it in conjunction with the evolution of diagnostic *Pinus* seed cone characters (Ryberg et al., 2012) or was it uncoupled? During the Early Cretaceous, the Pinaceae underwent an explosive evolutionary radiation that included a wide range of *Pinus*-like species (Smith et al., 2016). If evolution of the seed cone can be taken as a gauge for wood evolution in *Pinus*, then a diagnostic suite of characters for *Pinus* wood (including axial resin ducts with thin-walled epithelial cells) probably evolved over a period of several million years with those characters accumulating one-by-one during that interval (Ryberg et al., 2012). Seed cones of extinct *Pinus* and *Pinus*-like Pinaceae (including many *Pityostrobus* species) occupied a much broader range of morphospace than do living *Pinus* species (Smith et al., 2016). If the same was true for wood characters, and combinations of wood and seed cone characters for extinct Pinaceae, then it is highly probable that some *Pityostrobus* species had wood that is indistinguishable from that of living *Pinus*. Uncertainty exists regarding the utility of single wood characters for distinguishing between extinct species of *Pinus* and the sister group (or groups) of *Pinus* during the time interval when the genus was undergoing its initial radiation.

We conclude that *P. yorkshirensis*, from the Hauterivian–Barremian transition (Ryberg et al., 2012), remains the oldest record of *Pinus* and that '*P.*' *mundayi* is not demonstrated to be a species of *Pinus*. We maintain that Pinaceae evolved during the Jurassic (Rothwell et al., 2012) and that evolutionary diversification of *Pinus* was well under way by the Early Cretaceous (Smith et al., 2016). We suspect that stratigraphically older species of *Pinus* remain to be discovered, but emphasize that to be accepted as such, discoveries need to be placed within rigorous stratigraphic and systematic frameworks.

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Supplementary Information

Systematic interpretation of characters of ‘*Pinus’ mundayi* as described by Falcon-Lang et al. (2016)

	Character	Systematic significance
1	Long-shoots, 3.6–4.2 mm in diameter and <17 mm long, preserving pith, primary vasculature, secondary xylem, and (locally) phloem	Not diagnostic of *Pinus*
2	Stellate pith, 1.15 mm in diameter, composed of axially elongate parenchyma, cells 100–120 μm high and 20–25 μm in diameter	Not diagnostic of *Pinus*
3	Profuse pits on all walls	Not diagnostic of *Pinus*
4	Eustele comprising ~20 endarch primary xylem patches (Fig. 1C), composed of scalariform tracheids, ~10 μm in diameter	Not diagnostic of *Pinus*
5	Secondary xylem, 1.2–1.4 mm in radius, comprising one or two rings of growth, each ring being composed of thin-walled earlywood tracheids, 10–25 μm in diameter, that pass centripetally into thick-walled latewood, 10–15 μm in diameter	Not diagnostic of *Pinus*
6	Earlywood tracheids show 1–2-seriate, circular, bordered pits, 10–15 μm, with circular apertures, and opposite arrangement where biseriate	Not diagnostic of *Pinus*
7	Latewood tracheids lack pits or show sparse, circular bordered pits only	Not diagnostic of *Pinus*
8	Rays uniseriate, 1–11 cells high, and lack ray tracheids	Not diagnostic of *Pinus*. Ray tracheids are characteristic of living species of *Pinus*
9	Cross-fields of ray parenchyma showing 1–4 fenestriform or pinoid pits	Not diagnostic of *Pinus*
10	Few scattered axial parenchyma strands occurring close to axial resin ducts	Not diagnostic of *Pinus*; present in a few species such as *P. hartwegii* Lindl., but more common in species of *Abies* and *Larix*
11	Thin layer of secondary phloem, <350 μm in radius, locally adhering to outer-most part of shoot	Not diagnostic of *Pinus*
12	Periderm not preserved	Not diagnostic of *Pinus*

Data:

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