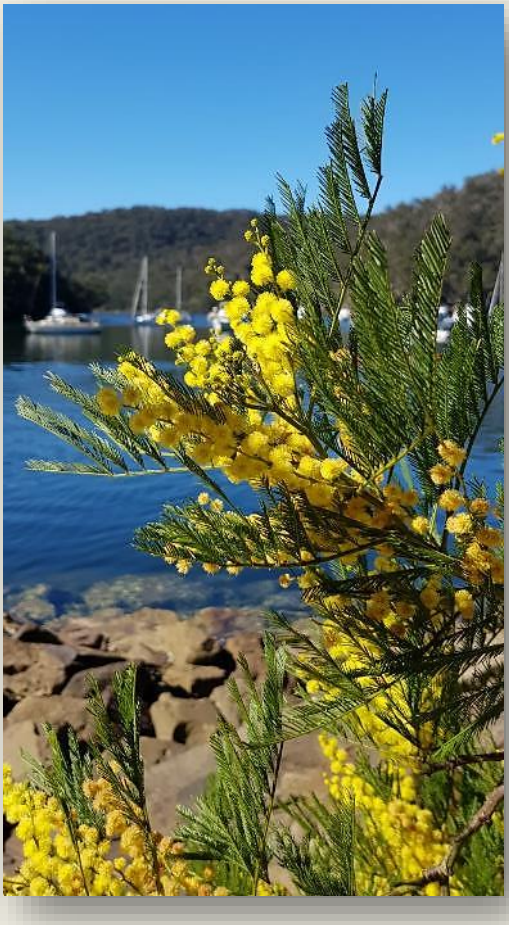
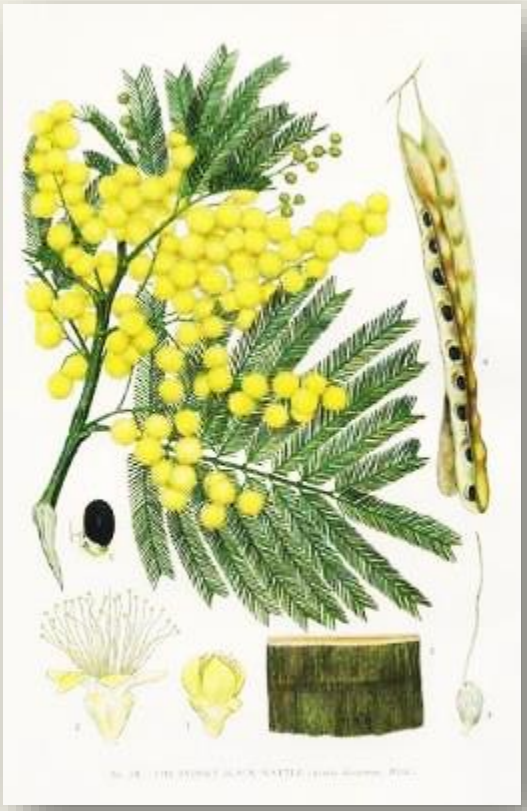
Acacia leaves - which came first, phyllode or (p)feather?



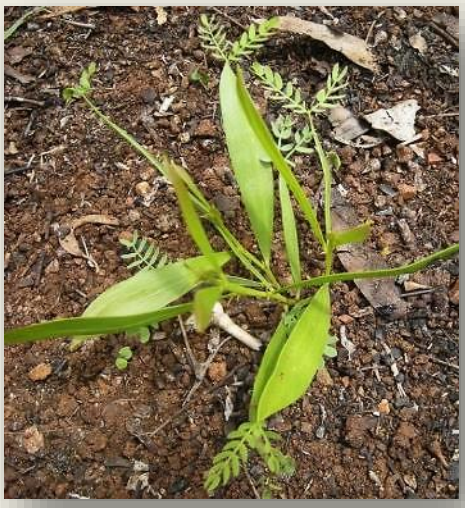
What better way to celebrate the end of a long, bleak, cold, wet winter in eastern Australia than to rejoice in the spontaneous appearance of glorious gold and yellow wattle? However, it's easy to overlook foliage when the grey green bush gives way to masses of brilliant flowers and yet the *leaves* of *Acacia*, rather than the flowers, are proving to be valuable tools in tracing the evolutionary origins of wattles in Australia.

There are two types of *Acacia* leaves: true leaves – the feathery ones; and *phyllodes*, which are flattened leaf stalks modified to function like leaves.

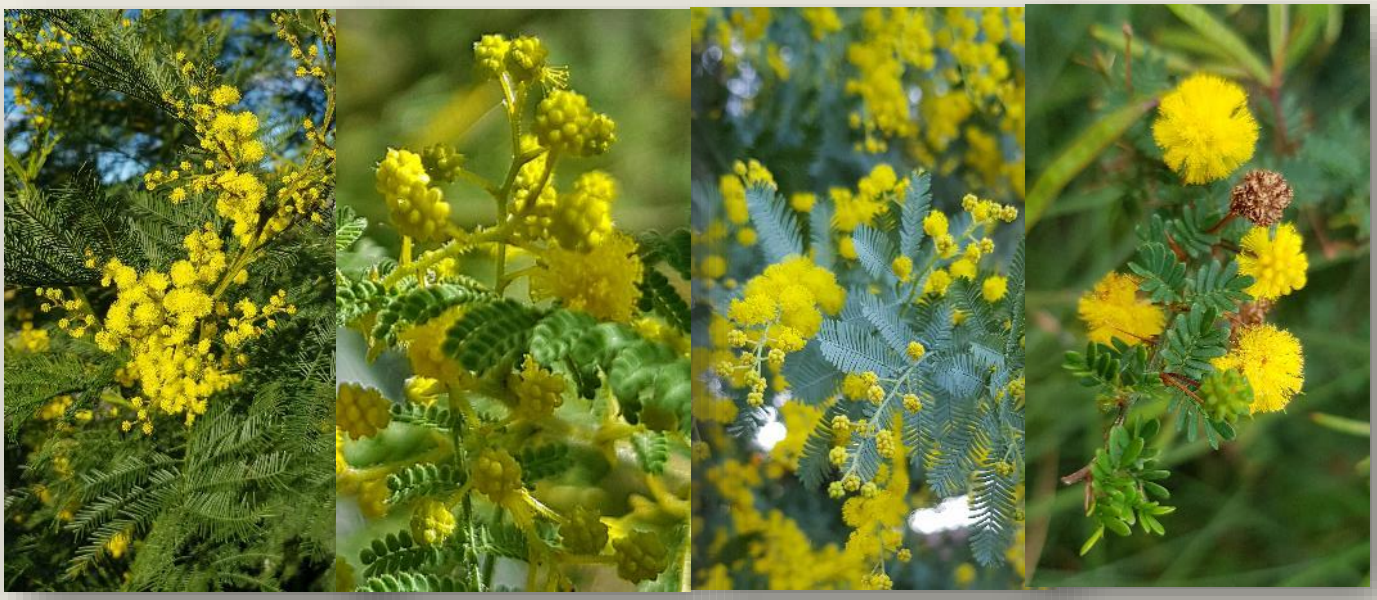
All young seedlings of *Acacia* have *bipinnate leaves*, some retain this characteristic all their lives. *Pinnate* refers to the feather-like structure of leaves (*pinna* – a Latin word for *feather*), namely a central stem (the *rhachis*), sometimes just one set of small leaflets attached along each side of this stem (*pinnate*), or a second set of smaller lateral stems with very small leaflets attached (*bipinnate* – or *twice pinnate*). About 10% of all *Acacia* species have bipinnate leaves.



Bipinnate leaves. *Acacia decurrens*, Green Wattle, by artist Edward Minchen *In* Maiden J H 1896.



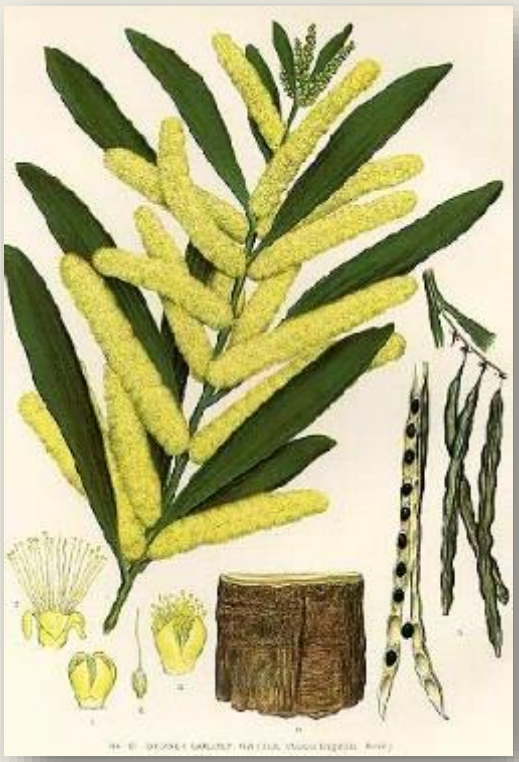
Acacia fasciculifera, seedling, showing transition from pinnate leaves to flattened phyllodes. Photo: Mark Marathon, CC BY-SA 3.0 <https://creativecommons.org/licenses/by-sa/3.0>, via Wikimedia Commons



Acacia species with bipinnate leaves. From left: *Acacia decurrens* – Green Wattle; *Acacia cardiophylla* – Wyalong Wattle; *Acacia baileyana* – Cootamundra Wattle; *Acacia browniana* – Browns Wattle.

However, juvenile bipinnate (feathery) foliage is quickly replaced in many species - ~ 90% - by *phyllodes.* (*Phyllode* – from Latin, *phyllodium*, and before that, from Ancient Greek, φυλλώδης, phullṓdēs - *resembling a leaf*). There is an extraordinary range of shapes and sizes in *Acacia* phyllodes, from small, spiny, needle-like structures, to broad, flattened leaf-like structures. Drought tolerant phyllodes are considered to be an adaptation to dry conditions facilitating the diversification of *Acacia* into drier environments and nutrient poor soils, more noticeably as the Australian continent moved northwards during the breakup of Gondwana.

The presence of bipinnate leaves in *Acacia* seedlings has been considered to be evidence that the ancestral *Acacia* had bipinnate leaves. This seems logical, as *Acacia* is the only genus within the Caesalpinoideae subfamily of the pea family, Fabaceae, to have phyllodes. (*Acacia* belongs in the Mimosoideae, now considered to be a *clade* within the Caesalpinioideae). All the other genera have pinnate or bipinnate leaves. Bipinnate leaves capture light more efficiently in low light environments, require fewer resources for growth, and have higher rates of carbon dioxide uptake and higher photosynthetic rates than phyllodes and also tend to grow in cooler, wetter environments than wattles with phyllodes.



Phyllodes. *Acacia longifolia* Sydney Golden Wattle, by artist Edward Minchen *In* Maiden J H 1896.

A team led by Matt Renner, National Herbarium of New South Wales, questioned whether the bipinnate-leafed wattles we see today reflect that ancestral state, or whether they had evolved more recently. They found that the *most recent common ancestor* of *Acacia* probably had phyllodes, not bipinnate leaves. (*Most recent common ancestor* means the *most recent individual from which all*

Acacia species with phyllodes. From left: *Acacia echinula* – Hooked Wattle (Photo: Sarah Schuler); *Acacia longifolia* – Sydney Golden Wattle; *Acacia melanoxylon* – Black Wattle; *Acacia binervia* – Two veined Hickory.

present-day individuals are directly descended). So, although the earliest ancestor of all *Acacia* species is considered to have had pinnate or bipinnate leaves, the *most recent common ancestor* of *Acacia* probably had phyllodes. Transitions between phyllodes and bipinnate leaves have occurred in at least three different lineages of *Acacia*, and within each there have been reversions back to phyllodinous adult foliage. Extant species with bipinnate adult foliage acquired this from phyllodinous ancestors, mostly quite recently, between 5 million and 1.5 million years ago. This may have been in response to wetter and cooler conditions along the Australian coast during the Pliocene.

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Maiden J H 1896. *The Flowering Plants and Ferns of New South Wales – Part 4.* NSW Government Printing Office.

Renner M A M, Foster C S P, Miller J T, Murphy D J. 2021. Phyllodes and bipinnate leaves of *Acacia* exhibit contemporary continental-scale environmental correlation and evolutionary transition-rate heterogeneity. *Australian Systematic Botany* 34(6): 595-608. https://doi.org/10.1071/SB21009

Summerell B. 2022. The Cutting Edge. Evolution of *Acacia* leaf adaptations. *The Gardens* 134: 11.

Wikipedia: https://en.wikipedia.org/wiki/Cyclamen_persicum

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